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An Exploratory Study on African Lions

JOSEPH B. COOPER, Ph.D.
San Jose State College, San Jose, California

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AN EXPLORATORY STUDY ON AFRICAN LIONS

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ACKNOWLEDGMENTS

This monograph describes the methods and results of an investigation conducted at the Gay Lion Farm at El Monte, California, which the writer presented as a dissertation to the Graduate School at the University of California at Los Angeles, in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Psychology, in the Spring of 1940. The writer wishes to acknowledge his gratitude to Professors Knight Dunlap and Howard C. Gilhousen for their assistance throughout the study and in the preparation of the manuscript. The writer's appreciation also goes to Professors Franklin S. Fearing, Roy M. Dorcus, Raymond B. Cowles, and Herbert S. Jennings, for their criticism in the formulation of the problem and presentation of the findings.

BACKGROUNDS FOR THE STUDY

There is a general lack of information concerning *Felis leo.* There are no published accounts, consistent in approach and technique, dealing with sensory capacities, perceptions, learning, or any typical behavior corresponding to accepted psychological categories. Furthermore, there are no adequate accounts on typical organized patterns of behavior such as maturational functions, sexual responses, maternal behavior, play, etc. However, there is scattered and uncritical material on all these subjects.

An observational study of captive lions was undertaken with the particular intention of investigating the following behavior categories: (a) Activities Preliminary to and Following Feeding, (b) Training Responses, (c) Vocalization, (d) Adult Play and Fighting, (e) Sex Activities, (f) Gestation, Parturition, and Infant Care, and (g) Characteristics of the Lion Cub.

Basic to the initial conception of this research was the belief that a thorough preliminary study of an observational nature would accomplish two things. First, it would contribute two types of relatively precise material: (a) descriptions of procedures for the study of a species, which could be duplicated for other closely allied species, and (b) descriptions of behavioral patterns of a species which could be compared directly with those of other closely allied species. Second, it would contribute clues to certain important experimental problems, and offer suggestions concerning the most expedient procedures for their investigation.

The particular advantage of the observational approach has its basis in the facts that general behavior patterns and organizations of activities are of great concern, and that it is highly important to know what actual type of stimulation a species seeks and what kinds of patterns occur in the process. In this field, the observational method may "go beyond" the limits of experimentation, since it can show organizations of patterns in time, their initial phases, their continuation and extent, into what they lead. Moreover, certain types of activities such as fighting, vocalizing, maternal behavior, mating, courtship, etc. which can not be said ever to occur "naturally" under laboratory conditions, hence can be studied only by cautious observational techniques. In addition, the observational method frequently may be employed to advantage with those species not amenable to the usual laboratory equipment and situation.

Comparative research varies between the extremes of the completely experimental and the completely observational techniques. Examples of comparative investigations which have employed both procedures may be cited. For instance, Stone (25) has investigated congenital sexual behavior in rats, employing controlled, experimental conditions. However, it is significant that some of the most important items in this, and other investigations using a combination of the two methods, were obtained by simple observation. For the organized, pattern-type activities toward which Stone's studies were directed, observations under relatively controlled conditions were most suitable. Further, the work of Coronios (7) on the development of behavior in foetal cats has contributed some incidental information on oestrual behavior which was obtained by the observational method. Experimental procedure is not appropriate to this type of activity if the investigator is interested in describing the complete behavior. Kohler's (17) extensive investigations of anthropoid behavior represent an integration of the experimental and observational procedures.

Carpenter's (6) completely observational study of the gorillas at the San Diego Zoological Gardens is a close analogy to the present investigation. His investigation, though considerably shorter than the present study in extent of time, was, like the present, an attempt to describe just what certain animals do under the conditions that have been set up for them. In order to make these observations, to keep them in line with psychologically significant phenomena, and to make adequate descriptions of the behavior observed, Carpenter observed in terms of certain behavior categories.

Two sources of information have been consulted in the present investigation: literature sources, and the observational locale, the Gay Lion Farm at El Monte, California. The body of this monograph will be concerned with descriptions of

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observations made at El Monte. Reference to relevant items from the published sources occasionally will supplement these descriptions. However, the collegation of representative information on lions, which has been one of the purposes of this investigation, will not be reviewed here.

INFORMATION CONCERNING THE HABITATS AND ANATOMY OF FELIS LEO

Omitting the earlier history of the rise of the carnivores, it is known that in the Oligocene, the differentiation of the modern carnivores was well under way. The various groups of particular importance were: civits, hyenas, saber-toothed tigers, weasels, dogs, raccoons, bears, certain aquatic carnivores, and the cats.

The cats still have certain affinities with all the carnivores, but may be regarded as the most specialized forms. With few exceptions (e.g., the cheetah which has unusually long, thin legs, and non-retractible claws) they are very similar skeletally, though they vary greatly in size. For example, the skeletons of the lion and tiger are almost indistinguishable, and these two species sometimes mate and reproduce.

The origins of modern *Felis leo* are obscure. Abundant remains of *Felis spelaea* have been found in Old World and European Pleistocene deposits. *Felis spelaea*, long believed to be a distinct species of *Carnivora*, has been shown by Dawkins (8) and others (21) to be nothing more than a large variety of *Felis leo*. This large variety is frequently called the "cave lion" and is entirely extinct now. This animal inhabited Britain, Sicily, Spain, France, Germany, Switzerland, and Belgium during the post-glacial period, and was a contemporary of the "cave hyena," and "cave bear." Lubbock (20) says that remains of *Felis spelaea* have not been found in Scotland, Ireland, nor in the Scandinavian countries. He reports the finding of the remains of a species at Natches, Mississippi, which was called *Felis atrox* (a new species, supposedly). The characteristics of these remains are strikingly like those of *Felis spelaea*. If there is actual identity here, *Felis spelaea* must have gone east across Russia and Siberia, where no such remains have been found. Inasmuch as the reindeer, bison, and most of the quarternary mammals occur also in America, Dawkins and Sanford (21) may be correct in maintaining that *Felis atrox* and *Felis spelaea* are identical and were present on both continents. The "cave lion" (*Felis spelaea*) undoubtedly survived into the earlier part of the human period in Europe.

It has been maintained by some authorities that if it were not for the encroachment of civilization, *Felis leo* would still live in Europe. Others say that it would not, claiming that it moved to more southernly regions with the encroachment of cold. Johnson (16), presumably indicating that the lion avoids cold regions, maintains that it never ascends higher into mountains than about 3,000 feet. However, this observation was made in only one district, and it certainly does not hold for many regions in East Africa. There is another objection which can be made to the retreat-from-cold theory for the migration of the lion. Dawkins (8) has pointed out that, among all the mammals living in Europe in the Pleistocene, the hyena is the only one other than the lion which is now confined to more southernly regions.

It is probable that neither of these theories completely explains the lion's migration and that a number of factors, other than those they embrace, will in time be found to have relation to the geographical occurrence of the species. This problem deserves attention. Incidental references will be made in the following account to points which seem to throw some light on its preliminary consideration.

The time of the extinction of *Felis leo* in Europe has been estimated variously from about 500 B.C. to the beginning of the Christian era. As to the occurrence of the lion in other areas of the world, there are many items of information scattered in the accounts of travelers, hunters and others, and in the representation of the lion in art forms. The following digest does not pretend to cover more than a part of the information which is available.

Though *Felis leo* is known to exist today in various parts of Western Asia, its chief habitat is Africa. At one time it seems to have ranged all over this continent. However, within recent time, it has disappeared from certain African districts. It is almost extinct in Egypt, and seldom appears along the Mediterranean coast, in the Gaboon and Niger districts, or near the Cape of Good Hope (21). (The Boers have long been famous as lion hunters, and have managed to free the Cape region almost completely of the animals.)

Most of the available information pertaining to the lion in the wild state comes from the central and east African areas. Herbert Lang, in particular, has made interesting observations upon the lion in the wilds. More lions may be found in the lower Sudan, Kenya, Uganada, Tanganyika, Mozambique, North Rhodesia, South Rhodesia, Bechuanaland, and the upper portion of the Union of South Africa, than in all of the other habitats combined. The Kreuger National Park is one of the most heavily populated lion habitats in the world. This park is located in what might be called the heart of the lion country, northwest of Swaziland, and only a few hours' drive from Johannesburg or Pretoria. It is approximately 500 miles inland, and north of the seaport of Durban. It consists of about 8,000 square miles, and affords almost every variation in climate. If an actual native-habitat field study of *Felis leo* is ever conducted, this probably is the best location in the world for such a study.

Despite the fact that the lion apparently has been extremely rare in India, there are almost as many references in the literature to the Indian lion as there are to the African. The former occurred at one time over wide areas of central, west, and northwest India (5). It was claimed in 1891 by Blanford (2) that in general the lion had been restricted in India to ". . . The wild tract known as the Gir in Kittywar . . . (with) a few more in the wildest part of Rajputana." Burton (5) writes that the only Indian locality in which they may be found today is Janagada in Kathiawar. He also claims that they probably occupied most of the whole of central India at one time. Within the last hundred years they have occupied a region extending from Harriana (north) to the south and east of Guzerat. Up to 1860, lions were seen in central India (much south of their present limits) and east of Allahabad. In 1922, one was shot in the Katah State. The Sinh Darwaza (lion gate) of Jaganath bears a large effigy of a well maned lion, killing an elephant. Records show that the lion hunt was the favorite sport of Babar, who is known to have hunted lions on the banks of the Indus, and in the vicinity of Benares. Blandford (2) attests that in about 1870 lions were common near Mt. Abut, Gevalior, Goona, Kata, and Jhansi. He has records showing numbers of animals seen and shot in north-east and central India.

It is claimed by Blanford that east and north of India the lion is not found. However, as will appear, there is some evidence to the contrary.

Though the lion probably has been found most extensively in Africa and India in the last five hundred years, it, of course, has occupied other regions during this period of time. It is claimed by Geikie (12) and others that the lion still remains in certain localities in Asia Minor and Persia. In 1914 Wright (31) reported its current presence in regions surrounding the Persian Gulf. There have been a number of reports that the lion has been seen within recent years west of the Euphrates. Wright (31) claims that it still is found occasionally in the Mesopotamia Valley. Some writers claim that the lion was common in the region around Palestine until the time of the Crusades. As late as 1850, the carcass of a lion was brought into Damascus (21).

There is conflicting evidence concerning the lion's presence in China. The problem is complicated by a number of factors. First, there apparently has been at least an occasional lack of differentiation between *Felis leo* and the "Pekingese" canine. A number of travellers and explorer historians writing on the subject evidently have been confused by the two animals' similarity in sitting position, shape of the face, and "mane". The striking contrast in the size of the animals suggests the theory that the Pekingese may have been regarded as a "small" lion and that in speaking of it as a "lion," the writers were but following custom.

A second factor in the complication of this problem is the task of evaluating the sources. It is unusually difficult to do so since many of the references are from "travel-marvel" literature, which was written to startle and amaze the reader.

A third factor which complicates an attempt to discover whether or not the lion migrated into China, is the fact that frequent importations of lions into that region have been recorded. Despite the fact that these problems of approach exist, examples of available material, presented with the above appropriate qualifications, are not without some significance.

Although there is no recorded confirmation, it may be conjectured, because of certain geographical limitations, that if the lion migrated into China and became native there, then at some time before the Christian era, it occupied certain areas as far north as the Kirghiz Steppe. Lacouperie (18) is the source for evidence that lions were imported into China from the west, early in the Christian era. He says, that at that time "Several such missions or embassies . . . from the west . . . have been recorded in history. . . . The Arsacidae in A.D. 87 sent lions. . . . In A.D. 101 the king of Banku of Ansih . . . sent lions. . . ." In 87 A.D. and again in 101 A.D., a Parthian commission arrived in central China with many goods and gifts, among which were lions. It is said that the country of Tiao-tchi, near the Western Ocean, reproduced lions, but whether or not they were *Felis leo*, and whether or not they were produced by domestic breeding, is not known. At the present stage of investigation of this problem, it appears that the lion was introduced into China by man.

Concerning the gross anatomy of the lion, there is considerable information. The body of the adult male lion is about five and one half to six and one half feet long, including the head. The tail is from two and one half to three feet in length. It stands about three to three and one half feet high. Females are proportionately smaller. The tail is well tufted at the end, with a small horny point (well hidden by the tuft), which seems to be an outgrowth of the skin. There are 24 or 25 caudal vertebrae.

The lion's skull is thick, heavy, and massive, with a broad zygomatic arch and well marked sagittal and occipital crests. The superiod surface of the skull is remarkably flat. The postorbital processes are in almost the same plane with the forehead. The posterior termination of the maxillary bones, on the face between the orbits, is opposite the end of the nasals. The exposed portion of the presphenoid bone in the mesopterygoid fossa is very narrow and is usually flat. The lower edge of the mandible is convex, owing to a small projection below the hind-most and lowest molar. The skull of one adult male has been measured at thirteen inches across the zygomatic arches.

There are five digits in the manus, and the hallux of the pes is reduced to a rudiment of its metatarsal. The middle digits of the pes are longest. The distal phalanges have claws, and the phalanx which supports the curved claw is also curved. A plate of bone arises from the base of the phalanx as a short sheath for the retracted claw. An elastic ligament connects the base of the ungual phalanx with the middle phalanx, so that when the *flexor profundus digitorum* is not in action, the ungual phalanx is pulled back upon the middle phalanx, and the claw which it bears is retracted into the integumentary sheath.

The dental formula of *Felis leo* is: I.$\frac{3}{3}$, C.$\frac{1}{1}$, Pm.$\frac{3}{2}$, and M.$\frac{1}{1}$. In some cases there are only two upper pre-molars, and occasionally there are three lower premolars. The upper carnassial has three lobes and a small inner tuberole; while the corresponding lower tooth has no inner cusp or hind talon (15).

The lion's brain cavity is not large. The olfactory bulbs are relatively large, and cerebral hemispheres are rather elongated. The cerebellum is practically encased in a bony sheath, and is relatively small. The medial fissure of the cerebellum is only vaguely visible. The lion's eye pupil is oval, and the iris muscle in the adult is yellow-tan. The infant's pupil tends to be elliptical, converging at base and vertes, and the iris is tan-grey.

The lion is tawny (yellow-brown) in color. Often the belly and medial parts of the legs are lighter in color. Cubs are usually marked with rather deep, dark spots, or bands, in irregular designs. Most of these darker markings are found on the back, the tail, over the face and head. Females, in particular, frequently carry some of these spots into adult life. Adult males have heavy names (varying in length) being usually lighter in color close to the body, and growing darker (almost black) more distal from the body. The mane usually grows from the crown of the head all around the neck, and in some cases drops down to the ventral side of the belly. Females never have manes. On both males and females the tufts on the outside of the ears, and the tail tufts, tend to be black.

It should be pointed out here that the hyoid bone, supporting the larynx, is a ligament furnishing the larynx with more motive power and thus affecting the voice. In the smaller cats, the hyoid bone consists of a series of short, pointed bones, allowing less motive power. Only the larger cats can emit roaring noises, the smaller can "mew" and purr.

DESCRIPTION OF CONDITIONS FOR OBSERVATIONAL STUDY

Numerous places are to be found where lions are raised and trained; various zoos, menageries, and circuses maintain lions. In the main, however, these establishments are inappropriate to an extended observational study. Zoos, which afford the best opportunities of the three, usually support but a few lions, and the small number of animals and cramped quarters result in very infrequent displays of many types of significant behavior. For example, few zoos actually breed lions, and this alone significantly limits the range of behavior.

The Gay Lion Farm at El Monte, California, which is owned and operated by Mr. Charles Gay, furnishes an ideal opportunity for an observational study of semi-domesticated lions. Mr. Gay's interest in scientific investigation has been shown by his continous cooperation in permitting and helping in the arrangements for special situations which made possible the collection of much of the material to be cited.

Mr. Gay began raising lions in 1919, with an initial stock of one male and two females. Since then the stock has been increased considerably by importations, but most of the colony of nearly 200 animals was born at El Monte.

The purposes of the farm seem to be four: sale of animals, sale of hides, special training for show and cinema work, and providing instruction and entertainment for visitors to the farm.

The farm covers five acres, and is equipped with extremely serviceable apparatus and buildings. The lion houses are of two general types: inside individual compartments for individual feeding and night shelter, and outside enclosures for groups. A system of runways which can be swung into place when animals are to be moved, connects the inside compartments with the outside enclosures. Various groups usually occupy the inside cages during the mornings and are fed there, while other groups occupy the adjoining enclosure-lots. In the afternoons these groups are interchanged.

The age range of the animals is from new-born cubs to animals of about 20 years, but the largest proportion are about eight years of age. The sexes are approximately equal in number.

The lions are segregated according to several principles. Young animals between five and eight months are taken from their mothers and housed together. They remain together until they are about 24 months old, and are then divided into sex-groups. Sex groups thus formed are not again divided or added to, except for periods of individual isolation necessitated for feeding, breeding, parturition, training, and for prevention of fighting.

Throughout this monograph considerable attention is given to the more significant conditions which existed at the El Monte farm. Many of these conditions still obtain and may provide an opportunity for further studies. It is, likewise, possible that parallel conditions might be created for other feline species and valuable comparisons obtained.

I. Activities Preliminary to and Following Feeding

At the Gay Lion Farm behavior related to feeding represents one of the most regular and easily observed activity phases. A definite feeding schedule is followed, by which each animal (except the younger cubs) is given a portion of raw horse flesh once a day at a regular time. On Mondays none of the animals (except the younger cubs) are fed.

A typical feeding-day routine will be described here. Each enclosure-lot has its accompanying cage-compartment. The males are kept in one end and the females in the other end of the individual cage compartments during the night. Each morning the attendants remove one of the sex groups to the outside enclosure, and move the sex group still inside, back and forth, for the purpose of scrubbing the individual cages. After these procedures are completed, the doors between the compartments are opened and the animals still inside are free to move from one cage to another. At a definite time, the attendant comes with a wheelbarrow containing chunks of horse meat. Each animal is by then securely locked in a single cage compartment, after which the attendant goes past each compartment and throws a portion of food to each animal. From here, the attendant goes back to the butcher shop for more meat and repeats the same procedure with another group located at some other place on the farm. At a particular time after the feeding of the first group, the attendant returns and removes the bones which remain. He then exchanges the inside group (already fed) with the outside group (not fed yet). Then he arranges the animals of the incoming group in individual compartments and feeds them according to the same procedure described above.

The highly regular nature of the attendant's routine is reflected in the accurately timed behavior of the lions. Many individual and group patterns which are built up, in terms of these specifically performed and timed routines of the attendants, are described in detail below. These patterns are initiated and sustained by hunger demands and the feeding routine.

Though adult animals exhibit relatively individualized and specific patterns prior to feeding, some of the pre-feeding performances are relatively characteristic of all animals. The most typical behavior, shown by animals in the outside enclosure, is pacing. Usually about twenty minutes before these animals are to be taken inside to be fed, one of the members of the group gets up from its resting position and begins to walk slowly back and forth, always on the side of the enclosure adjacent to the feeding compartments. Within two or three minutes, another animal gets up and follows and within a short time all the members of the group are milling back and forth in front of the gate through which they will go into the compartments. Pacing becomes more and more individualized and vigorous as the time for feeding approaches. Finally, certain members of the group run back and forth along the fence, while others go to the gate and paw and strike it. When the attendant arrives to pull the gate up, the entire group is at the gate waiting, and when the gate is opened, the entire group tries to squeeze through at once. It is frequently necessary to open the gate only high enough for one animal to push through at a time, in order to prevent a pile-up of animals and a possible fight. During this pre-feeding period the lions are in such a state of "tension" that fighting frequently occurs.

In the other situation, where a group has been placed inside some time before being fed, the patterns of response are quite similar. At approximately twenty minutes before feeding time, the animals begin pacing inside the cages. When the attendant comes with the food, all the animals rush to the end of the cages closest to him. Finally, they go to their "own" compartments and the attendant walks past the compartments locking the doors between them. This same sort of "compartment selection" may be observed in the case of groups that are brought from outside just prior to feeding.

The generalized and specific pre-feeding patterns shown, together with "compartment selection," are evidence of habits which are dependent upon feedings and food demands. Since these patterns start and reach their height of intensity at just about the time the animals are fed, these displays are, therefore, of an anticipatory nature.

If the usual routine activities of the attendants are disrupted, the normal pre-feeding reactions of the animals are not shown. When feeding is delayed, the animal's patterns changed markedly. One day the attendant was fifteen minutes late in feeding a particular group. When the actual time came for feeding, the animals were pacing vigorously. The pacing patterns increased in intensity, and were gradually restricted to the end compartments closest to the place where the attendant first came into view at the normal feeding time. As was stated before, when the attendant arrives the animals select their own compartments and are locked in them. But, since the attendant had not appeared, this selection had not taken place. This crowding into the end compartments restricted the possible floor space, prevented pacing and other typical pre-feeding responses, and in moving about the animals bumped into each other considerably. At about twelve minutes past the normal feeding time, hissing, growling, clawing and striking became increasingly frequent. Before the attendant arrived a relatively serious fight had taken place. Since fighting almost never takes place inside a cage (as will be elaborated in the section on Adult Fighting) it is reasonable to suppose that this display of fighting represented a serious condition of upset. As soon as the attendant arrived (now fifteen minutes late) the disrupted behavior stopped, the animals ran to their own compartments and waited to be locked in them.

These learned anticipatory pre-feeding activities are undoubtedly dependent upon existing spatial and temporal stimulus sequences. If the above situation could be duplicated experimentally (i.e., with adequate controls) several important aspects of the relationship between these pre-feeding patterns and the related stimulus sequences might become apparent.

This specificity of pre-feeding behavior can be accounted for in terms of secondary cues which are present. That is, the various attendants on the farm keep up a rigorously repetitive routine, and noises and figures passing here and there on the farm constitute the "stimulus pattern" for the animals. On Mondays the animals are not fed; and on that day no animals display pre-feeding behavior. This indicates that the usual routine is the stimulus pattern necessary for pre-feeding behavior. However, the observation reported in the previous paragraph (describing the fight) does not fit in with this description exactly. In that case these secondary cues were slowed up fifteen minutes, but the pre-feeding activities were still displayed and by the time the usual secondary cues were presented an altogether new sort of pre-feeding pattern was going on. Nevertheless, the secondary cue description can still be employed, if it is assumed that the cues which really set up the usual pre-feeding display are not the adjacent ones, but are cues of earlier origin in point of time.

In particular groups, not all of the members of the group can be accommodated in the individual compartments which accompany the outside enclosure. Thus, several of the members of the group must be left in the enclosure while the rest of the group is taken in to be fed. It can be witnessed daily at the farm that, in such cases, certain animals of the group remain quiet (sleeping, or resting) while all the others are rushing hurriedly back and forth in their typical pre-feeding patterns. When the gate is opened for the animals-to-be-fed to come in from the enclosure, these not-to-be-fed animals still remain quiet, not responding in any observable way to the stimuli affecting the others.

In certain situations it has been observed that animals refused to eat meat that was offered to them out of schedule. Also, in one instance, when an animal was brought into a strange cage and offered meat, it paid no attention to the meat. These instances likewise point to the relatively specific nature of both the preparatory and consumatory phases of the responses which are sustained by food demands.[1]

As was stated above, there are significant individual differences in pre-feeding activities to be observed among these lions. When still in the outside enclosures, individuals perform relatively individuated pacing and pawing activities. As they crowd around the gate (which admits them to the feeding cages) certain animals become "socially" dominant, while others perfect repetitive patterns of an avoidance nature. Whereas one animal takes twelve paces to and from the gate, another animal may follow the former and take several avoidance steps when the former turns around. When they are let into the compartments, this sort of performance becomes somewhat more stereotyped, in accordance with the increased confinement and the more specific orientation to food. As each individual is locked in its specific cage, highly stereotyped patterns appear. Each individual displays a particular series of characteristic performances. Some face the front of the cage and violently tread with their front feet; others sit upright and paw the doors; others beat their heads back and forth against the front bars; others turn around in circles; while still others remain motionless and fixate visually upon the approaching attendant. Of course, there is, in most cases, a considerable amount of variation to the above itemized performances. That is, one animal may work several such performances into one lengthy pattern. Though there is a great deal of noise set up by the animals at this time, due to contact with the cage, very little vocalization accompanies this pre-feeding activity. Roaring appears to have no direct relation to pre-feeding activity.

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[1] "Food demands" is employed here to mean the same as "drive," as employed by Skinner (23). He says, "The *drive* is an hypothetical state interpolated between operation and behavior and is not actually required in a descriptive system."

In terms of modification, all these activities preliminary to actual eating seem to be responses set up to "fill in" the time which elapses between the appearance of the initial stimulus pattern and the actual eating process. As Thorndike (28) has pointed out: "If we confine a cat, opening the door and letting it out to get food only when it scratches itself, we shall, after enough trials, find the cat scratching itself, the moment it is put into the box. . . . The association is formed with such an 'unlikely' or 'incongruous' response as that of scratching. . . ." This phenomenon is capable of description in terms of several known principles of learning.

As has been pointed out previously, lions show preference for visceral material over regular flesh. After the usual feeding of flesh, various groups (the individuals still in their compartments) are given about two pounds of visceral material each. The lions maintain a demand for this material only about two weeks at a time. That is, after being given it for a two weeks period, they will no longer eat it for a time, but will prefer it again after a two weeks interval.

Within a day after being started on this second ration of food (i.e., the visceral material), the consumption of regular flesh is followed immediately by a second display of pre-feeding behavior. The typical beating of the doors and bars continues until the visceral food is given; but after this second feeding, pre-feeding patterns are not begun again. Synchronously with the failure to eat the visceral food, the second display of pre-feeding behavior usually disappears. However, the relationship between the pre-feeding display and the demand, is not as precise as might be anticipated. In some cases, animals carry out a second display of pre-feeding behavior, even though they will not eat the visceral food when it is given to them. It is probable that this second display is dependant upon secondary cues which are still present.

These pre-feeding activities have a relatively definite development with age. When cubs of about five months are taken from their mothers and put together to form a large group, they are introduced to an exclusive, one feeding per day, meat diet. This new regime is accompanied by the development of the pre-feeding activities already described. But the patterns at first are much less distinct and less individualized than adult pre-feeding patterns. Within a short time after the new regime has been started, restlessness just prior to eating may be observed. If the cubs are outside prior to eating, they begin to run back and forth in front of the gate. When they are admitted to their individual cages (which they very soon learn to pick out) they usually stay far back in them and vocalize considerably. (This vocalization is in the nature of low, sharp barking.) They also remain far back in their cages while eating. Though it takes some time for these young animals to develop specific individualized patterns, it is extremely obvious that just prior to, and during, eating they undergo a condition of severe upset. These generalized upset responses represent the first system of performance which become associated with the feeding process.

To return to the adults, individualized processes are distinguishable also during the actual process of eating. Usually, just as the attendant reaches for the meat to be thrown to an animal, that animal comes forward very close to the front bars and remains almost motionless, fixating visually upon the meat. When the meat is thrown under the base board, the animal drops down and quickly draws it in with its forepaws, at the same time grabbing the meat in its mouth. It then lies down close to, and facing the front bars, holding the meat under its paws, and begins to pull off chunks of the meat with its teeth. Each chunk, thus pulled off, is swallowed without being chewed, and each swallow is accomplished by a ducking motion of the head. Occasionally an animal licks the meat all over before actually eating it. Tough tendons and fibers are cut with the molars. This is negotiated by a lateral bending of the head. When visceral meterial is fed there is practically no mastication.

About six animals on the farm are always fed the heads of horses. The attendants say that they try out various animals on the farm on horses heads, and that very few are able to break the bones open and get all the meat out. Those that are found to be "skillful" at this are from then on given the heads regularly. This indicates considerable individual difference in the actual eating process.

During the eating process (as was stated before) there is practically no vocalization. However, in most cases, active gestures by a human close by will occasion a series of loud growls. In such instances, upon getting his food, the lion usually picks it up in his mouth and strikes through the bars with his fore paws at the disturbing person. This same sort of performance occurs whenever another lion comes into sight during feeding.

All the animals on the farm have access to water when they are in the outside enclosures. It is estimated by the attendants that adult lions consume approximately one pint of water per day. They show a distinct demand for water just after eating, and during very hot weather their consumption of water increases considerably. Drinking is negotiated by a lapping motion of the tongue, with the lower jaw often submerged in the water, and might be described qualitatively as "leisurely." In some instances, when females are being watered together just after feeding, minor fights occur. This has not been observed in the case of males.

II. Training

The published material which has to do with the training of large animals is relatively abundant. However, this literature is usually not of any actual value to the psychologist. For the most part it consists of narrative descriptions of stunts performed, and not of descriptions of the processes involved or of the conditions which obtained during the learning process.

Likewise, the direct observations of lions in training at the El Monte Farm throw little, if any, light upon the psychological nature of learning. For the most part, these observations have been made on already established habits, and it has not been possible to investigate the speed of learning, learning capacity, or other related aspects of the modification problem.

The methods and concepts which lie back of the actual training of lions are largely of an empirical nature, and are not based upon any particular knowledge or interest by the trainers in the learning process or its conceptual implications.

No psychological descriptions of training of tigers, lions, leopards and other big cats are to be found in the literature. Theoretically, the factors affecting this type of training should be no different from those affecting the learning process in other species. Practically, the size and presumable fierceness of most of these animals make it necessary to impose training conditions which tend to obscure the very factors in which the psychologist is most interested.

These imposed conditions vary according to the type of stunt required of the animals. However, in terms of the incentives which are set up to establish and maintain these performances, they are of two general types: food incentives and avoidance-incentives. The descriptions which follow concern the varying conditions which are imposed, the types of incentives used, and the nature of the performances themselves.

One male that was in training at the time of these observations was about seventeen months of age and had been in training for a particular stunt for about ten months. This stunt was to climb upon a stand, dangle its legs over an attached rail, and *vocalize* into a microphone which was held up for it. General training had been going on since early signs of docility were recognized. When the cub was only a few days old it was taken from its mother and raised in the house on a bottle. During its stay in the house it began to vocalize frequently. This consisted in "mewing," which soon increased to extrordinary proportions just prior to each bottle feeding. At the same time, the cub remained extremely gentle, and unusually active and responsive. These combined qualities led Mr. Gay to put the cub into an individual compartment and arena when it was about six months old. For the next few weeks different people on the farm visited the cub daily and played with it for rather long periods. Also, before each bottle feeding the trainer who did the feeding would wait until the cub had responded with this particular vocalization. When actual training for the desired stunt was begun, it was an easy matter to hold the bottle on the side of the stand opposite the cub, and get the cub to climb up on the stand for it. However, before the bottle was given to the cub, it was required to vocalize. This sequence was picked up very quickly to the point that as soon as the trainer entered the arena the cub climbed upon the stand, and when the bottle was shown, began vocalizing. Placing the microphone before the cub evidently has no relation to the performance whatsoever. At the time of these observations he was fed a bottle of milk each hour throughout the day as a reward for his trick. He was also given a large portion of meat at 5:00 p.m., when the day's routine was over.

Essentially, there are very few elements in this whole process which are not "worked out by the cub himself." This is the type of training which consists of waiting for the act and then giving a reward. The act is elicited relatively easily by the limitations which are imposed upon the animal. These limitations consist of reducing the number of responses that the animal can make, and thus raising the probability of appearance of the responses needed for the trick. Furthermore, the reward which is given upon the completion of the correct sequence tends to establish the sequence.

The second performance to be described is that of a five-year-old male. This animal was also raised in a cage in the house and fed on a bottle. It had been in training since it was slightly over a year of age, and had been fondled and played with since it was a very small cub. This animal performed several tricks. One of these was climbing on a barrel and rolling it back and forth across a lot, by treading. Another trick consisted of climbing up to a platform, from which two cables were stretched to another platform. The animal was then required to walk across the cables, pick up a stick in its mouth which it carried until told to drop it.

In contrast to the positive food reward incentive for the vocalizing trick, the dominant incentive here is avoidance, that is, avoidance of the trainer's threats. In order to create this situation the trainer must establish a "prestige value" for himself with the animal. With this established, the trainer is able, by threats, to restrict the animal's field of action to the point that a certain pattern is "hit upon." When the desired pattern *is* "hit upon" the reward of being "left alone" is given. This means a widening of the animal's field of action, and a resumption of usual behavior (such as lying down, sleeping, etc.). The animal soon learns to perform the desired response, or sequence of responses. Fondling, petting, etc., seem to be of no value in reenforcing such a correct response sequence.

Procedure for training a group of lons is essentially similar to that used in training the five-year-old male described above. Though there is some evidence to the contrary, the trainers maintain that imitation is an important factor in group training. They say that if they are able to get one animal to go through a particular pattern they find it much easier to obtain similar patterns from other members of the group. Groups never perform as intricate tasks as do single animals. No observations have been made of trainers petting and wrestling with animals in groups, as is frequently done with individually trained animals. Moreover, trainers always carry whips (also revolvers) when training groups. The purposes of the whip seem to be two; first, it is occasionally expedient to "sting" an animal to break up hesitation; second, the whip's "crack" often has the effect of startling animals into action.

In any training situation the trainers maintain that it is always dangerous to take food (meat) into the arena. (This is occasionally done, but it is always carried in a leather case, and is used as a reward for only one animal of the group on some individual trick.) They also say that it is dangerous to use physical force to compel an animal to do anything, or for the trainer to give up until the desired pattern has been elicited. Further, they state that it is never advisable to strike an animal severely, to run while in the arena, or to turn one's back on the animals.

Females are seldom trained. This is said to be due not to inferior ability, but to their smaller and less spectacular appearance.

It is maintained by the trainers that cubs give certain indications as to whether they will become suitable for stunt performance. These judgments by the trainers are based upon vague criteria for the degree of such capacities as: good general appearance and activity, responsiveness, docility, etc. For example, of a group of cubs, certain ones are recognizably more docile than others, even though they have been raised under similar conditions. Docility, of course, is an important quality for a stunt animal. Again, some cubs are "alert," quick, adept at running, jumping on things, and coming when called. Others are noticably deficient in one or more of these types of response. That a cub shows these responses is no sure indication that it will maintain them until it is old enough to be trained. Unless it is frequently handled and petted, the chances are that it will be too wild when it is old enough for training. When cubs are about one year of age, they usually lose much of their "playfulness." With this loss, comes a state of "reserve," and only then can training actually be started.

III. Vocalization

Vocalization is one of the most common features of lion behavior. For convenience, the most evident types of vocalization may be divided into the following recognizable classes: roaring, growling, hissing, barking, and mewing.

Some observations will be described which will show the relationships between types of vocal expression and the various conditions under which they occur. Sound and motion picture equipment would be required to identify and differentiate precisely between types, and to indicate clearly the patterns, intensities and durations of these various vocalizations. Likewise, prolonged and careful observations would be required to accumulate essential data on periodicity, sex differences, dominance, group responses, etc., in regard to the different types of vocal expression. Among other problems which arise in relation to this behavior province are the important developmental sequences through which cubs go in arriving at the adult vocal stage.

Roaring is the most frequent, most noticeable, and probably the most variable type of lion vocalization. Usually, animals are standing during roaring, but almost any usual body position may be assumed during this activity. An animal may be lying on its side with its head flat to the ground, or may be sitting up, or even lying on its back. Very rarely do animals walk while roaring. They often take a step or two and roar several times, and repeat this procedure. But when an animal begins roaring it almost inevitably comes to a standstill. Vigorous hoisting and lowering of the diaphram is always evident, and is an integral component of the raring function. An individual's roaring begins slowly, increases to a maximum frequency, then decreases as gradually as it began. The pitch remains almost the same. An individual continues to roar for about forty-five seconds. No matter what bodily position the animal may be in, the head is usually thrust forward and up. The jaws are a bit open and relaxed to the extent of vibrating with the sound. The noise is in the nature of a rumble, each series of rumblings being one expiration. While it cannot be definitely established, it appears that the larger the animal, the more its roaring resembles rumbling, and the deeper the pitch. Individuals seem to be impervious to shouting and demonstrations by humans during roaring. Occasionally, however, some very unusual and abupt stimulus may disrupt the roaring of an individual.

During the daytime, group roaring takes place about every forty-five minutes. One animal begins to roar, and this is followed by another and then still another, until a great part of all the animals on the farm are roaring together. Such group roaring lasts usually for about two or three minutes. There are various combinations in which such group roaring takes place. That is, sometimes all the animals of the particular group will participate. Sometimes group roaring may be localized to one part of the farm, while at other times it may be widespread.

Group roaring is somewhat more frequent during the early morning than at other times of day. About an hour before sundown roaring is especially frequent.

Roaring does not seem to produce any specific effects upon other animals. The exception here, of course, is that some animals respond to roaring by roaring, and some do not. There seems to be no relation between food-getting and roaring. Also, there seems to be no typical relations between sex behavior and roaring. That is, neither males nor females roar just prior to, or following, sexual behavior. On the other hand, copulation between a male and female is occasionally followed by group roaring. In the final act of coitus, the male usually vocalizes in a "bursting"-growl. This seems to be a stimulus pattern capable of producing group roaring; also, any fight that may occur among adults on the farm is always followed by group roaring. The fighting animals always growl fiercely and loudly, and this intensive growling seems to set off roaring in other animals, more than any other given condition. During a serious fight, in which there is considerable growling, group roaring is decidedly above normal. Also, it lasts longer, and the individual's vocal contributions seem to be shorter and louder. Instead of a series of rather long, rumbling expirations by individuals, the expirations are shorter and more intense.

For a time during these observations, it appeared that certain "leaders" were responsible for group roaring. Since then, more extensive observations have clearly indicated that an individual may be a leader at one time but not at another. Also, it was believed in accordance with earlier observations, that only males were successful in starting group roaring. This, too, has been shown to be false, by more extensive observations. Though males are more frequently "leaders," females do, occasionally, start group roaring.

There are few sex differences with respect to roaring which are obvious enough to be detected by crude observation. Of course, as has been indicated, males are slightly louder and lower in pitch than females. It also appears that males roar somewhat more frequently than females. As a final act in coitus, as has been said, the male emits a loud bursting growl, which it appears, is qualitatively different from any other vocal expression given by male or female. Females exhibit several vocalizations which are disimilar to male vocalizations. During the œstrual period females accompany their pacing and rolling with series of low growls much like "gargling." This is typical of œstrual behavior. During copulation, this same noise becomes continuous and turns into a sharp growl-hiss at the final moment of the act. Frequently, when females are pacing during the latter part of the gestation period they emit vocal expressions quite similar to the "mews" of a domestic cat; though, of course, they are much lower in pitch. The periodicity of these low "mews" seem usually to follow the pattern of the pacing. This same sort of "mewing" is frequently exhibited by a mother with her cubs. Usually when this happens, the mother seems to be attending in some specific way to her cubs.

Growling is probably an "emotional expression." From the quick, spitting or bursting growl to the slow, rumbling kind, there is evidently involved a tightening up of the sternal muscles and a mobilization for quick, intensive action. There seem to be no obvious sex differences in growling.

Infants begin vocalizing at about nine or ten days. This first "vocalization" is really a hissing noise which is released while snarling. Later the "mewing" expression develops, and by the time the cubs are taken from their mothers, this has dropped considerably in pitch. When cubs are taken from their mothers (from four to eight months) they soon begin pre-feeding pacing. This pacing is frequently accompanied by "mewing." The "mewing" seems to be definitely in rhythm with the pacing. Young animals begin growling in particular situations very soon. Often when a mother is licking a cub, the cub continuously growls and hisses. It is reported by the attendants at the farm that males as young as five months have been known to roar. This has not been observed in the present study, however. It appears that males begin to roar earlier than females, or at about twelve months of age, and females at about fourteen. For both males and females, roaring usually develops into the typical adult type between the ages of twelve and eighteen months. It also seems that as animals grow older they roar more. But it appears that when lions are about fourteen or fifteen years of age roaring becomes relatively infrequent, and that it is most frequent at about the age of eight years.

There is a common belief that lion roaring is a form of communication. This study has not aimed at proving or disproving this belief, and it is impossible to reason conclusively from the data at hand regarding this question. However, it is, of course, evident that the validity of this belief rests entirely upon one's definition of communication. If we define communication broadly as, "reaction to, and production of, patterns of sound as symbolic meanings," it would be necessary to show that these types of reactions occur in the lion. When one lion rushes toward another, the second's behavior is modified, and in terms of the behavior of the first. This is not responding to a symbol, it is response to a direct stimulus change. When a lion roars, other lions may roar also. It cannot be said, however, that either the original roaring or the subsequent roaring of the other lions are symbolic responses. Though Learned (19) and others have been able to distinguish various distinct vocal sounds made by a chimpanzee, these sounds have never been shown to carry any symbolic meanings. Though it is quite evident that, under certain conditions, lion vocalization will produce changes in the behavior of other lions in auditory range, it can not be claimed that this is communication, if communication is defined as above.

IV. Adult Play and Fighting

Play among adult lions is a relatively infrequent activity. It is, of course, difficult to define play accurately, and it is often difficult to identify the pattern, when it appears. It frequently is impossible to distinguish between play and fighting.

Incidental psychological descriptions of play behavior may be found in the literature. A display of play behavior may be identified by certain criteria. The organism engages in play at a time when no definite maintenance demands must be met (13). Sequences of responses usually are pursued which employ elements of responses used in the acts of fulfilling necessary bodily demands. There is usually a rapid shift from the use of one such element to another element. The consumatory phase of a response pattern is not present, and only the preparatory elements are in operation. According to these criteria, certain activities will be described which are arbitrarily called play.

Play occurs most frequently following an important change in the environment. For example, play is frequently participated in by animals just after they have been released from their inside cages into the outside enclosures. It has also been noticed that the presence of one of the attendants may be followed by a display of play activity. At other times adults will engage in play with members of their group that have just been released into the enclosure. That is, several animals may be in an enclosure while two or three others are being confined inside to be fed. When these two or three are released, others of the group may play with them. It appears that play is also somewhat more frequent shortly before pre-feeding activity is begun. Before the pre-feeding behavior is begun, occasionally one or two of the members of the group may go from animal to animal, rubbing, sparring, etc. Playing is considerably more prevalent on cool, brisk days than on warm days. It is much less frequent during the middle of the day than in the early morning, or in the evening.

As nearly as can be judged, females play more than males. Females occasionally play with their cubs. Frequent twitching of the tail is typical of females with cubs; the cubs chase and bite the mother's tail. It is probably true that play is somewhat more generalized in the case of females than in the case of males. That is, a greater variety of stimuli will call out play in females than in males. The usual types of behavior which females display during the oestrual period, such as rolling, pawing their ears, rubbing and trying to get beneath other females, etc., are often confused with play by the casual observer. The greatest difference between play and patterns relating to the oestrual period is one of duration; the oestrual patterns persist considerably longer.

From the age of about one month to about one year, there is an increasing frequency of play. From about one year on, there is a progressive diminution of playing. By the time a male lion is four years old play is conspicuously infrequent. Though relatively rarely, some females persist in occasional displays of play until they are ten or twelve years old.

As will be described more fully in the section, "Characteristics of the lion Cub," the inter-group responses of lions appear to be essentially different from those of certain other species. In the case of domestic cats, for example, playing usually consists of a rapid shifting of responses, first toward one animal and then toward another; one kitten darts at another kitten, slaps, rushes toward another, and so on. In the case of lions, responses are almost always made to one particular lion, and such activity is by no means always reciprocal. One adult engaging in play usually follows another particular animal around, jumping on it, etc., but does not respond directly to other members of the group.

Isolated young adults may sometimes be seen playing with various objects in their cages. This type of play usually amounts to pulling and clawing at the object. The young male mentioned in the section on "Training" often playfully tugs on the stand that is in his arena. In fact, until the stand was staked down to the ground he would pull it all over the arena. Isolated animals play less frequently than animals in groups, however.

There are some individual differences in the play responses of lions. One series of observations brought this point out very clearly. Three large males, each about ten years of age, were kept in three separate cages. On a number of occasions the observer ran a stick along the edge of each of their cages. The first lion made no attempt to grab the stick, but simply followed it visually and occasionally struck at it lightly, without extending his claws. The second male struck savagely at the stick, struck through the bars at the observer, growled, and showed "typical anger." The third male made no response to the stick at all. In view of the fact that these stimulus patterns were presented a number of times, and were responded to characteristically by each individual, but differently by the three, it may be assumed that these responses represent real individual differences. The activity of the first animal would be designated as play; that of the second as rage. The individual differences in play are in great evidence among the males. However, although females play considerable more than males, it appears that individual differences among them are considerably less pronounced. Of course, there are some evident differences among the females. For example, when one of the trainers walked by one group of females, one member of that group characteristically ran along the fence, jumped, turned, and demonstrated typical play activities, while none of the others made any distinguishable responses to him. When females are confronted by novel stimuli, such as a person running back and forth in front of the enclosure, they crowd around, push each other, climb on each other, etc. These responses appear to be play responses. Males very seldom respond at all to stimulus patterns of this nature.

The most frequent play pattern of adults involves stalking, running (which becomes more important as a feature of play as they grow older) and leaping upon the backs of other animals. If there is some sizable object in an enclosure, an animal engaging in play often gets behind the object (so that the object is between itself and the animal being stalked.) The stalking animal then sways its body back and forth, lashes its tail laterally, holds its head very still and out far enough to fixate visually upon the other animal, and lowers its hind quarters slightly. This process continues until the animal turns its back. Then the stalker dashes across the enclosure, and, providing the other lion's back is still turned, jumps on its back, gives it a glancing bite, and dashes away. Sometimes the other animal pursues the stalker. If the other animals happens to turn around while the stalker is running across the enclosure toward it, the stalker usually stops still and discontinues the pattern, or it may stop quickly and dash off in some other direction.

Rolling and biting is less frequent among adults than among cubs. Sometimes an animal persists in a great deal of play-running, and is jumped on by the other animals; this occasionally turns into minor fighting. It seems that any rapidly moving object, whether it is a bug, a human, a stick, or another lion, catches the attention of lions, usually to the extent that they will chase it. Such pursuit is not always play, however, and in many situations it is impossible to identify the pattern.

It may be observed from the foregoing descriptions that all of the patterns which have been designated as play, are conceivably patterns which are employed in the negotiation of "fundamental" activities. Any of these responses, transferred to different situations, might become integrated into fighting, hunting and killing prey, biting off meat and chewing it, sexual patterns of various types, etc. It is possible to conceive that were enough known of these types of behavior just mentioned, the essential role of what is ordinarily called play might be more adequately understood.

The patterns of activity which are described here as fighting, seem to be capable of more objective identification than were the activities which were designated as play. For convenience, lion fighting may be defined as a series of responses, rapidly executed, and of the following types: (a) rapid series of growls; (b) offensive bodily surges with wide, open-claw, fore-paw strokes; (c) lateral-forward head movements, with jaws open, and constant snarls with the lips and tongue rolled back; (d) violent bodily shaking whenever in contact with another animal; and (e) rapid shifting from place to place within the limits of the enclosure. When these patterns are rapidly executed and elaborately intermixed (none, of course, are mutually exclusive) they can be recognized readily as fighting.

The most conspicuous fighting responses are made with the fore paws. The animals make swinging, sweeping strokes, delivered in most cases to the head regions of another animal. They approximate a sitting position, and the rear legs are used for springing and manipulation. However, when three or more animals are involved there are great variations to these patterns. Fighting is always accompanied by baring the teeth, snarling, tail lashing, lowering the hindquarters, and growling. The snarling and growling which accompanies this behavior invariably is followed by general farm roaring.

Some of the conditions under which fighting takes place will be described. Some writers claim that lions live in troops, and that one dominant male is the stud for all of the females in the troop. They also maintain that every so often there is a "grand fight," and that the former dominant male may either retain his "right" by winning the fight, or may be deposed by another. As will be pointed out in the section on "Sex Activities," when a group of males is with a group of females (some of which are in oestrus) only one male (usually the largest) courts and copulates, and displays dominance. This may very well be one of the conditions that will lead to fighting.

Although under usual captive conditions lions will always fight over food, no accounts have been found of their fighting over food in the wilds. It is probable that lions sometimes do fight over food in the native habitat, although, under the usual native conditions, they probably are able to obtain more food than in most captive conditions, and, thus, have less hunger drive. Moreover, in the native state, a large animal usually is killed, and two or more lions can eat on it without interfering with each other. In the captive condition, meat is always cut up into relatively small pieces, and two animals could not eat on the same piece. In captivity, even small cubs will occasionally get into scraps over a small piece of meat.

Under the conditions of captivity, unless lions are raised together from the time that they are cubs, they can never be housed together without continuous and serious fighting. If a lion is introduced to a group to which it is a stranger, it is attacked by the entire group. This situation has been observed several times during the present study. Females must be isolated from their groups during the latter part of the gestation period, and for several months after parturition. When this period is over and a lioness must be put back with her sex-age group, it is necessary to confine the returning female with each of her original group members for a night, until she has been reintroduced to all of them. She is then turned out into the enclosure with the whole of the original group. It is characteristic for the other females to jump on her and spar with her, but there seldom is a serious fight. Likewise, in the case of males, it is necessary sometimes to isolate them. In such instances, the same reintroduction process just described for females must be followed.

It is maintained by the attendants at the farm that lions will not fight in the cages. However, as was pointed out in the section dealing with feeding behavior, one minor fight was seen to take place within the cages. The attendants are probably correct, nevertheless, in saying that serious fighting will not take place in close quarters. The attendants also say that if two strangers are housed together, they will begin to fight as soon as they get into an outside enclosure.

It seems, then, that there is a direct relation between the size of the field in which the lions are situated and the frequency and amount of fighting.

It is possible that strange or unfamiliar objects serve as stimuli for fight responses. As was pointed out, introduction of a strange animal to a group is responded to by fighting. On several occasions, strange objects, such as an old automobile with dummies in it, have been put into an enclosure, and as soon as the lions were released, they characteristically have rushed up to these objects and torn them to pieces. As will be pointed out in the section dealing with cubs, even cubs respond with vague fight responses when a newcomer is brought into the group.

Due to enforced celibacy, or to other factors that are unknown, male lions fight more frequently than females. Thus, when males reach sexual maturity, some of them display homosexual behavior. This amounts to courtship, mounting and attempted copulation by one male toward another particular male. The display of homosexual activity may last for several days, and during that time, any other male in the group that happens to come into close physical contact with either of the courting males, is apt to be attacked by the one displaying the aggressive homosexuality. Other members join in and usually attack the interfering male. This condition is responsible for the most frequent and intensive fights that take place under the conditions described here.

It is a curious fact that the other members of the group attack the interfering male and not the aggressive homosexual male. This might be thought of as a matter of group dominance; that is, that the other members will not attack the aggressive homosexual male, since, in all these cases, it is the dominant animal in the group. According to some accounts (mentioned in the first part of this section) fighting is usually centered about dislodging the dominant male of a group. But the matter of dominance is probably not seriously involved in the present question. Rather, because the dominant homosexual male usually attacks the interfering male very abruptly, and in most cases knocks him down, it would seem to be more a matter of the other animals jumping on one that is "down," than actually "picking sides."

When the whole group is engaged in a fight, various combinations and differences of attack may be observed. The group generally attacks one animal. The object seems to be to get it down and to tear its body, particularly in the head and throat regions. Such fighting usually lasts only for a few seconds. The male which is attacked by the rest of the group is almost always able to break loose from the rest of the group and to run to the other end of the enclosure. He is usually followed by one or two of the group, but after a short sparring contest, accompanied by some growling, they all quiet down.

V. Sex Activities

Sexual responses are generally regarded as among the most important of all the classes of patterned activities of mammals. Without regard to any other types of behavior, sexual responses represent a domain of behavior fundamental to the existence of the species, and to the "well being" of the individual. With regard to other types of behavior, sexual patterns are seen to be intimately related to all such domains as fighting, play, vocalization, food getting, etc.

Observations on sexual responses reported here have been centered principally on: the development of sexual behavior in both males and females; behavior during the estrual period; sexual excitement in males; courting behavior; copulatory responses; and, "homosexual" behavior.

Sexual maturity is reached in captive lions at about 26 months. It has been impossible to determine whether or not there is any real sex difference in the time of appearance of sexual maturity. The question is complicated by the relatively definite response patterns shown by females in the estrual phase, and the more obscure, unstable male patterns. It is not difficult to identify an estrual behavior pattern. But males perform their sex patterns (mounting, etc) only when females come into the estrual phase. This leaves the possibility that the males are sexually mature before females. Various control methods might be employed to determine the onset of mature sexual behavior in males.

It is the usual procedure at El Monte to separate animals into sex groups at about 24 months. In a recent situation males and females (about 23 to 27 months old) have been left together. In this situation two females have come into estrus (both at about 27 months) and all the males attempt to copulate. This indicates the maturity of all the males in the group but not of all the females.

Male cubs as young as three months have been observed mounting various other members of their age group. Not all male cubs display this pattern, but those that do point to the probability that this male function has a very early genesis. It has been observed with fair accuracy that such young males do not have erections during these mounting performances.

Males begin to show manes several months prior to what this study suggests is the onset of sexual maturity. This secondary sexual characteristic continues to grow, however, for a considerable time after sexual maturity appears. Males also show a definite widening in the shoulders (not present in the females) and a general body growth beyond that of the females. The forelegs and paws, in particular, show an increase in size out of proportion to the fore-legs and paws of the females.

During this period of change, a sex difference may be noted in general activity. The females remain more active than do the males. The males spend more and more time sleeping and lying still, while the females do considerable walking and pacing. Also, the females show greater general responsiveness to humans in their visual range. Provided no females are in the estrual phase, the responsiveness of males and females to each other appears to be about equal.

The behavior of lionesses during estrual periods is markedly different from their behavior during non-estrual periods. Characteristic patterns of activity are carried out, essentially similar from animal to animal, and from period to period. Females raised in approximate isolation display the typical patterns of older females who have passed through several estrual periods.

As has been said, estrus first appears in females at from 24 to 28 months. Though it can not be quantitatively demonstrated, the general activity level during the first part of a female's estrual period appears to be considerably lower than that of the later part of the period. In contrast to domestic cats, which do much "calling," lionesses confine their vocalization to incidental rumbling and gurgling. At some heightened periods of tension, and usually during copulation, these noises increase.

The usual pattern of estrual behavior begins with a great deal of head rubbing and considerable deliberate contact with other animals. (These are females, of course, for no males are present.) This increases in frequency for several days, but is then gradually supplanted by other responses of the following descriptions: the female in question typically rolls on her back and pulls her hind legs up with her forelegs and bites them. She elevates and lashes her tail. The hind quarters are often "presented," which consists of swaying them, and elevating them while lowering the fore part of her body. During this type of display, she usually fixates visually on other animals close by. This type of patterned response is very similar to that of the domestic cat, as described by Coronios (7).

In cases of continued privation from males during this period, females respond sexually to other females and vigorously attempt to get beneath them. Pursuit is frequent, and the animal pursued often turns and fights off the pursuer. On two occasions, observations have been made of the following pattern: female A (in estrus) pursued female B (not in estrus.) During the pursuit A made lateral lunges at B's body. A also leaped a great deal and attempted to force herself under B's body. After being knocked down several times, B paused and A quickly crawled under her. B then assumed the role of a male and performed the characteristic, gross coital movements. This continued for only a few seconds, whereupon female B stopped and slowly crawled off of A. Female A then got up, slowly walked away and lay down quietly.

Regular breeding does not seem to reduce the length of a female's estrual period. Estrus varies in duration for different animals, lasting as long as two weeks for some and only a few days (seven or eight) for others.

Data were obtained from old records kept by one of the attendants at El Monte, relating to the time of the appearance of estrus. These records consist of the dates upon which females were bred, and the subsequent dates of parturition. With few exceptions, all females are bred when they appear in the estrus phase, and thus, while there is a slight degree of discrepancy in this data, for various reasons of farm procedure, these records accurately indicate the dates during which females were in estrus. Each female has a name, and when one appears in estrus and is bred, her name and the date are noted, along with the probable date of her parturition.

In regard to the estrual appearance, two questions arise: (1) does a particular female have a certain estrual rhythm (i.e., is there any consistency in her interestrual periods?) and (2) does estrus appear more frequently during one time of the year than another for the entire group of females?

The answer to the first question is complicated by several factors. First, frequently fertilization does not follow copulation, and consequently females come back into estrus and are rebred. Second, there are no control groups.

That is, no groups of females have been kept as non-breeders with records upon their estrual appearances. Further, since females do not always bear young as a result of a particular breeding, no knowledge of the effects of copulation (without subsequent parturition) is known. Despite these difficulties, it is possible to determine whether or not there is any rhythm in the appearance of estrus; on the one hand, for periods following breedings from which parturitions did not result, and on the other hand, for the appearance of periods regardless of parturition. Of the records of ten females studied, no reasonably exact periodicity (which might be called rhythm) was found. That is, to the question: "If a female is in estrus and is bred, with no resulting parturition, will there by any specific time before estrus will appear again?" a negative answer was found. There also appears to be no real consistency for individuals. From table 1 it can be seen that there is a range of from one to ten and one-half months (average) for individuals. In the case of female No. 9 it can be seen that there is consistency in the appearance of her estrual periods. On the other hand, female No. 7 ranges from sixteen to two months and female No. 8 ranges from twelve to one month. If the actual dates for every appearance of estrus were tabulated, regardless of subsequent parturitions, even less consistency would be found. It seems apparent that the physiological factors responsible for estrual behavior are not of a temporally rhythmic nature. It should be pointed out, also, that occasionally mothers still nursing their young (usually at about four months) go into the estrual phase.

TABLE 1

Intervals of time in months between appearance of estrus in ten females

The estrual period from which the time was calculated in each case did not, of course, result in parturition (El Monte).

	NUMBER OF FEMALE									
	1	2	3	4	5	6	7	8	9	10
	Months between estrous periods									
1st and 2nd periods...	2	7	2	2	1	4	14	12	1	8
2nd and 3rd periods...	5	4	1	1	1	5	16	1	1	3
3rd and 4th periods...		2	4			9	10	6	1	
4th and 5th periods...		1	1			8	2	3	1	
5th and 6th periods...			5			2		1	1	
6th and 7th periods...			1			1		7	1	
7th and 8th periods...			1			3		5		
8th and 9th periods...						3				
Average period......	$3\frac{1}{2}$	$3\frac{1}{2}$	$2\frac{1}{7}$	$1\frac{1}{2}$	1	$4\frac{3}{8}$	$10\frac{1}{2}$	5	1	$5\frac{1}{2}$

In answer to the second question: does estrus appear more frequently at one time in the year than another, a positive answer can be given. From 239 recorded cases of estrual periods at the El Monte farm it has been found that estrus is more frequent in the spring months of the year than at any other time. From the latter part of January to the middle of June the greatest frequency is found. Table 2 shows the exact appearances, in terms of the twelve months and in terms of the one half month periods.

Gebbing (11) reports some statistics from the Leipzig Zoological Gardens concerning the times of parturitions. His data was collected from 1899 to 1927. Though no data on the appearance of estrus *per se* is given, it can be computed by counting back three months and designating that date as the receptive period in that phase, and hence Gebbing's data can be compared with the present data. Moreover, his data is only for females that were in estrus and had subsequent parturitions. What data he gives (of 130 parturitions, see table 2) does not correspond with that from El Monte. Only in the months of September and October is there a significant drop in the number of estrual displays. Even selecting from the El Monte data only the estrual displays which resulted in parturitions (to correspond with the Leipzig data,) no significant correspondence may be found. Graph 1 shows the relation between these two sets of data, (i.e., only the estrual periods followed by parturition are recorded in both cases.)

Providing that these data are correct, it may be inferred that the greater climatic, seasonal changes in such a country as Germany do not affect the appearance of estrus. It is probable that were it possible to obtain the corresponding data from Leipzig (i.e., corresponding with the El Monte data) more definite seasonal variation would be apparent. It is difficult to believe that the estrual variations noted from the El Monte data are fortuitous.

TABLE 2

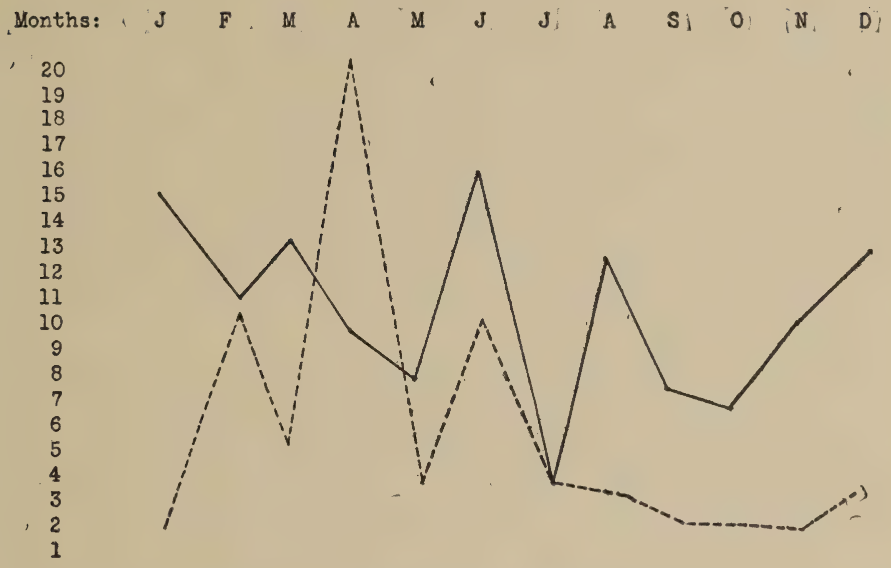
Number of times females came into estrus during the various months and one-half months

From 1931 to 1939; 239 cases in all (El Monte)

	JAN.		FEB.		MAR.		APR.		MAY		JUNE		JULY		AUG.		SEPT.		OCT.		NOV.		DEC.	
Month	17		36		35		33		25		27		10		17		10		9		15		10	
Half month	6	11	18	18	21	14	21	12	15	10	20	7	7	3	10	7	8	2	6	3	12	3	7	3

When sexually excited, males show patterned behavior which may be likened roughly to the behavior of females during the estrual period. As is true of females, males vocalize little during sexual excitement, and no definitely typical pattern of vocalization has been observed. Among the more obvious of these general patterns is the quasi-snarl, or sneeze-like grimace. This pattern consists of baring the teeth (especially the upper) though not opening the mouth very wide, and elevating the head (i.e., pointing the nose up). This display is always present just prior to feigned coitus, even in quite young males, and is always present and intensified during actual copulation. Almost always after a male has smelled the urine of a female (whether the latter is in estrus or not) this sneeze-like grimace is displayed.

As has been stated in the section of fighting, the celibate condition of most males predisposes them to atypical sexual fixation. By fixation is meant a display of courtship behavior by one male toward another, always to a particular



Graph 1. Shows frequencies of estrual appearance in 62 cases from the Gay Lion Farm (shown by dotted line) and 130 cases from the Leipzig Zoological Gardens (shown by solid line). Estrus dates graphed here were derived by counting back three months from the date of births given in the original data. This is not exact, but serves as the closest possible approximation. The El Monte data contained information on the appearance of estrus, but the estrus dates for El Monte on the above graph were obtained by the method just described. This allowed comparison of the two bodies of data, keeping the error constant in the computation of estrus dates.

TABLE 3

Number of times (Leipzig) females came into estrus during the months of the year

From 1899 to 1927; 130 cases

MONTH	ESTRUS OCCURRENCES
January	15
February	11
March	13
April	10
May	8
June	16
July	7
August	13
September	6
October	7
November	9
December	15

individual and lasting over a considerable time. These fixations vary in nature and in intensity. Most males do not acquire them at all. However, in the cases of males that do, the expression is almost always in the form of feigned coitus (i.e., mounting and immediate hip movements). One male devotes his attention to another male and attempts to copulate from time to time. Mounting is frequently attempted. As has been stated, in cases of this nature, any male that interferes with the two in any way is attacked by the aggressor male. Fixations of this type frequently lead to serious fighting in the whole group. Leaving the two involved males confined in a cage for several days usually results in the disappearance of the fixation, at least temporarily. It will be noted from the following descriptions that fixation behavior is essentially dissimilar to the usual male-female breeding patterns. However, descriptions of "free" courtship and breeding situation will be seen to parallel these male-male sex activities very closely.

Males that are regularly used for stud are isolated from other animals except at breeding time, and are housed at different locations on the farm, in order to facilitate the transference of females to the male's cages from whatever barn in which the females happen to be confined. It is not known whether this isolation is actually essential. No peculiar activities which might be thought to be related to the frequency of overt sex behavior are manifested by stud males. Like most older males, they sleep a great deal, roar with the rest of the animals, and carry on the usual patterns. Their responses just prior to copulation will be described below.

Courtship and copulation constitute a distinct phase of behavior. Under conditions in which males have free access to females that are in the estrual phase, courtship is a prolonged and definite type of behavior. Later in this section one situation of this type, in which males and females were all together in one group, will be described. However, under the typical breeding conditions that are regularly used at the Gay Farm, courtship plays a very minor role, and no attempt will be made to describe it apart from copulation.

Females usually remain in the estrual phase for one or two weeks. After a selected female has been in estrus for about four days, she is moved into a cage adjoining a stud male, and left there for a short time, usually less than half an hour.

When the attendant arrives to put the two animals together the female becomes very active. She growls, bares her teeth, turns, rolls, beats the door with her fore-paws, and lashes her tail. The male also increases his activity at this time. His demonstration also includes patterns of general restlessness, though considerably less than those of the female.

The attendant uses an iron bar to slide the door open about six inches. As soon as this opening appears the female inserts her paws and pushes until the opening is large enough to admit her. By this time, the male has retreated somewhat from the door, and the female rushes into his compartment. The attendant then pushes the door as far open as it will go to provide freedom in both cages.

The female is definitely the aggressor. At all times the male appears to be "on his guard" when the female is with him. The female frequently is bellicose, but only rarely does a male strike a female during breeding. Only infrequently does the male either lie down, or approach the female, between copulations. Moreover, the male does not mount until the female has adequately presented herself.

The following account describes a typical copulation. After the door has been opened partially by the attendant, and the female, with great excitement and force, has pushed herself through the opening and into the male's compartment, she literally drives, or lunges, under him. She lowers her head, growls, lays back her ears, and lashes her tail. Her hind paws are placed far back, about parallel with each other, and far apart. In this position she treads with her hind legs, while elevating her hind quarters. (The latter is accomplished partially by bowing her back.) At this same time she elevates her tail and turns it to the side. These responses are designated as the "presenting activity." Presenting seems to be the stimulus pattern for male mounting responses.

The male sidesteps the female, until she assumes the presenting position. His side stepping is usually accomplished while he keeps his body almost parallel with the female's. When the female has stopped whirling around, the male quickly lifts the front leg that is next to the female, and steps across her body to stand a little back of her shoulder blades. (His back leg nearest the female is usually brought *around* her hind quarters, not over.) He then elevates his own tail somewhat, turns his head to one side, and bites her neck. Erection occurs between the time the male mounts the female (i.e., steps across her body) and when he bites her neck.

During the mounting, the female vocalizes in a deep rumbling or gurgling; however, the male remains quiet. Most frequently, when the male has mounted, the female moves forward apparently to move out from under him, lashes her tail, and turns either partially or fully around. Usually the male is able to remain on top during this whirling. However, if the female stands up first, before she starts to whirl around, the male is forced to slide back quickly and avoid her. The female often turns on the male and strikes at him, and the male apparently is always on his guard for such attacks.

After the female has presented adequately, and the male has effected an erection, his sneeze-like grimace occurs. (To repeat, this consists of raising the head and elevating the nose, baring the teeth, and curling the lips with a resultant deep wrinkling of the face.) Characteristically, the male does not vocalize up to this point, except for occasional growls made in response to attacks from the female.

In case the female tries to alter her position after this time, the male may forego his grimace and bite the back of her neck again. The male does not make adequate genital contact immediately, even though the female lifts her rear quarters very high. His penis first contacts the female above and to one side of the root of her tail. As soon as this contact is made, the male begins hip movements from, and to, the female, about three or four inches each way. As this movement continues, the penis repeatedly contacts the female's body, each time at a point a little lower than the last contact. In so doing the male lowers his rear quarters into a squat position, while the female frequently raises hers. When genital contact is actually made, the male accentuates his grimace and begins to growl, while the female increases the volume of her vocalization. As this continues, the male's strokes become shorter, but appear to exert greater power toward the female, tending to raise her up. The male's body becomes more erect, increasing the distance between their heads, and at the instant his growl becomes a roar, he leaps backward and away from the female. Sometimes at this instant, the female whirls over on her back, before the male can jump away, and lashes him with her claws. In the cases in which he is able to jump back successfully, she turns upon him, clawing and hissing. (The male's responses to this are only of an avoidance and self-protective nature.) The female usually follows the male for several seconds thereafter, hissing, clawing, and biting at him.

After this display, the female usually retires to her original compartment. She throws herself down, turns on her back, and twists her torso profusely. Many incidental and persistent responses are performed during this rest period. For instance, she usually pulls up one, or both, of her back legs and bites her hind feet. Gradually she becomes quiet, and assumes a complete resting position. Such an inter-copulatory interval lasts for about five minutes. During these times the male maintains a standing position, apparently not attending to the female at all. However, upon any approach by the female, he either moves farther from her, or snarls.

After a lapse of time, the female suddenly jumps up, lowers her head and rushes into the male's cage. She elevates and lashes her tail. When in contact with the male she lowers her fore quarters and presents again. The male's behavior, as outlined above, appears almost identical each time.

Each actual copulation lasts from about 20 to 25 seconds. The frequency of copulation does not diminish appreciably as the period of cohabitation continues. In most cases, a male and female are left together about 45 minutes. The longest period observed was one hour and forty minutes. During this particular breeding period the animals copulated 20 times. The last eight copulations of this period began at the following times: 8:40; 8:43; 8:50; 8:55; 9:03; 9:11; 9:18; and 9:25. This approximate distribution has been recorded in several cases. For example, a different male and female left together for 30 minutes, copulated seven times. This is approximately once every five minutes. As stated above, the male mounts only when the female presents; therefore, the regularity and frequency of coitus can be said to depend upon the female.

The separation of a male and female that have been breeding is usually very difficult to accomplish. As soon as the attendant arrives and picks up the bar to pull the door closed between them, the male usually changes from his "submissive" behavior, rushes to the side of the female and will not leave her. It is often necessary for one attendant to go to the end of the cage away from the female and rattle something between the bars. When this is done the male rushes in the direction of the noise and another attendant quickly draws the gate closed. The female does not make any attempt to prevent the separation. The male often continues to growl, claws at the gate, and is generally "upset" for several minutes afterward.

Occasionally, copulation does not actually take place during the time that a male and female are allowed together to breed. Such failure to breed is usually due to inadequate presentation by the female. After several attempts at mounting, each being frustrated by inadequate presentation, the male begins to avoid the female completely, and turns from her each time she attempts to crawl under him. In cases of this nature no difficulty whatsoever is incurred in separating the two. Also, in cases in which the male is a novice, the male makes no attempt to prevent a separation. This probably indicates that at least some courting and copulating responses are subject to modification.

It is probably safe to say that there are very definite sex differences between the male and female in gross orientation responses in the breeding situation, in addition to the actual coition responses. The male performs the more stereotyped patterns of activity. Variations in his behavior from coition to coition are very slight. The above description of copulation has described typical response patterns of a male displayed toward an experienced female. When confronted with an inexpert, novice female the male's general pattern of reaction differs somewhat.

In contrast to the relatively stereotyped breeding patterns of males, those of females are variable. Virgin females are generally more restless. They do not respond adequately to males (i.e., they crouch but do not present). As soon as they crouch they leap up and whirl around. They usually are very bellicose, and frequently, after having "driven" themselves under the male, follow this with clawing, growling and striking. However, one or two experiences with a male usually are sufficient to modify their responses until presenting becomes adequate and actual coitus is effected.

A somewhat more quantitative and exact description of courtship and copulation is found in the following transcribed notes taken during an observation. The observation took place on March 15, 1938.

"Female was bred on 3/3/38, and since she was still in estrus, was put back in with male today, two days later. Put together at 7:50 A.M. After each copulation female rolls over and strikes male; cut male's nose. If female comes close to male within one or two minutes after copulation, male growls, bares teeth (snarls) and avoids her. Frequently, after copulation, female lies on back and pulls one hind paw up with front paws and bites it. Female frequently licks genetalia after copulation. Female goes to adjoining cage and growls at female locked there. Male remains standing, but female lies down, at various places, between copulations. During copulations, the male shows the typical sneeze-grimace, and continues this until ejaculation, presumably. Then he leaps back, with a loud, roaring growl, and female strikes at him. Male frequently starts to lie down, looks at female, growls, and then remains standing. Female presents well. Male bites back of her neck while copulating. When copulating, both growl more and more loudly. Female starts with "gurgling-rumbling," with increases in volume. Male begins to vocalize in middle of copulation, and at final instant his vocalization reaches greatest volume. Many other animals on the farm now roar. Copulations last from 20 to 25 seconds each. Pupil dilation is great during copulations. Before nineteenth and twentieth copulations, male went over to female, who was lying down, and licked her genitalia. Female began to move her tail, then jumped up and rushed under th male. They were separated at 9:30 a.m."

It has been pointed out that in the breeding situations which are created fo the animals at the farm, females are the aggressors in courtship and copulation and that males respond in accordance with the responses of the females. But in the descriptions of homosexual behavior among males, it has been shown that males take on aggressive functions, actually court, "protect," and aggressively mount. Though in opposition to the patterns of routine breeding situations this substantiates the contentions of some writers who maintain that males cour females in the wild state.

In contrast with the types of courting and copulating responses that have been described for animals under the routine breeding conditions at the farm one series of observations on an unsegregated (as to sex) group revealed patterns of an extremely different nature. As has been stated, lions apparently reach sexual maturity somewhere about two years of age. The group referred to here ranged in age from about twenty-three to twenty-seven months, but had not yet been divided into sex groups.

At the time these observations began, one female started to show estrual behavior. As soon as this display began, several males of the group began to follow her. Frequently they displayed the sneeze-grimace, and attempted to mount. The female snarled, hissed, and fought off such advances, no matter how persistent the male courtship might be. After about three or four days of such behavior (the frequency of these displays on the part of both males and females increasing from day to day) the female submitted to mounting. Her presentation was inadequate and actual copulation did not take place for the first part of this receptive stage.

The courtship consisted mainly in the males following the females (two more came into estrus in the meantime), nuzzling them, licking their genitalia, standing over them, and grimacing. The females continued to slap and strike at the males. Actual mounting took place almost as frequently as the females assumed anything like an adequate position. Copulation was less vigorous than usually had been observed in the case of older animals, under routine conditions.

Here, then, a group of sexually mature males and females were interacting. And here the dominance was the reverse of that under the routine conditions; the males were demonstrating aggressive behavior. However, copulation took place only when the female's bodies were in possible mounting position. Sex activities did not take place at all times during the day. There seemed to be certain periods when the females demonstrated estrual behavior and when the males showed sexual excitement periods. As nearly as could be judged, the excitement periods lasted about thirty minutes each and occurred about once every two hours. In addition, it is important to point out that the stimulus patterns which led to male excitement seemed to be most any and every response that an estrual female happened to perform. Also, whenever a male chanced to smell a female's urine, or nuzzled her genitalia, he usually became excited; and gradually, the whole group of males, and those females in estrus, showed sexual excitement.

It is significant that one male dominated the whole group. During excitement periods, when there was only one female in estrus, this one male (the largest of the entire group) followed that female about and was belligerent toward any other animal, male or female, who came close to her. When several females were in estrus, this male's dominance diminished. Frequently several males attempted mounting an estrual female, clumsily pushing each other off. No belligerence was apparent in these latter situations. Only the dominant male (referred to above) ever showed any real indication of "willingness" to fight.

While courtship and copulation are often thought to be a relatively stereotyped system of patterns, similar under most any conditions, the present observations point to the contrary. As may be seen from the foregoing descriptions, sex behavior is exceptionally varied, unstable, and modifiable, and conditions of the particular situation definitely are of importance in determining the resulting patterns.

VI. Gestation, Parturition and Infant Care

After copulation (if fertilization results) there is a period in which the female readjusts her responses in terms of non-estrus, and displays a system of responses not dissimilar to her pre-estrus behavior. Shortly before the parturition, however, females undergo certain alterations, both structurally and behaviorally. These behavior alterations are in a state of continual change from that time on, until the infants are taken away.

For reasons of descriptive facility the responses which follow copulation have been divided into three phases: gestation, parturition, and infant care. There is no way of obtaining data on the related activities of males during these periods, since males are never present with females after copulation. (Males that are present in cages adjoining mothers with newly born litters show no alterations in behavior.) Therefore, this section will deal only with females.

The length of the lion's gestation period is variously given. Sanyal (22) gives the tiger's at 106 days. Burton (5) has pointed out that Dr. Heinroth, of the Berlin Zoological Gardens, maintains that the lion's and tiger's periods are the same, three and one-half months. This would mean 105 or 106 days. Blanford (2) says that the lion's gestation period is 108 days. Brown (4) writes that the lion's period is exactly 111 days, and that the tiger's is 105 or 106 days. These various writers do not give statistics for their assertions. However, it may be assumed that their results are accurate for certain instances, but slightly inaccurate for lions as a whole. An average of their figures is approximately 107 days, with a range of from 105 to 111 days.

Some data have been obtained from the El Monte farm pertaining to the length of the gestation period in 51 parturitions. The average gestation period for these 51 cases was 109.74 days. The shortest period was 100 days, and the longest was 114 days. A frequency distribution shown by table 4 gives these gestation period durations. It may be seen by inspection that the mode is 110 days and the median is 106 days. Since the numerical average is between 109 and 110 days, and since the recorded date of birth is always made on the next morning, the average length of time would be about six hours less than the numerical average obtained. Thus, the average might be said to be approximately 109.5 days.

No great consistency in the length of gestation periods for individual females has been found. For example, of five females studied (picked at random, as a sampling), all of whom had had at least three litters, only one showed any consistency in the lengths of her gestations, that being a variation of one day. By simple inspection of table 5 it may be assumed that the length of one gestation period for one particular female has no relation to the probable length of any future gestation period. However, in contrast to the data in table 5, in a few cases studied the first gestation periods were longer than subsequent gestation periods of the same lioness.

TABLE 4

Frequencies of various gestation period lengths

LENGTH OF PERIOD	FREQUENCY
114	3
113	2
112	6
111	9
110	11
109	5
108	10
107	1
106	1
105	2
104	0
103	0
102	0
101	0
100	1
N....................................	51

All breedings, of course, do not result in fertilizations. Of 239 breedings at El Monte, between December, 1931 and September, 1939, only 93 resulted in parturitions. That is, 62 per cent did not, and 38 per cent did result in parturitions. There are a number of possible explanations for this low percentage of successful breedings; for instance, impotence on the part of the male, or ineffectual individual breedings. If ovulation is not spontaneous, and requires the stimulus of coitus to produce it, as is the case with domestic cats (9), the latter condition may obtain. However, in addition, it may indicate that the behaviorally receptive stage of the estrual period does most always correspond with the "fertilizability" of the ovum.

Occasionally, but very rarely, lionesses display pseudo-pregnancy. In one instance a female was bred, and after about 90 days began to show "heaviness." Soon after, she was isolated in a cage and preparations were made for parturition. All the gestation signs were present; e.g., pulling out hair around nipples, enlargement of the abdominal regions, enlargement of nipples, etc. However, she passed the normal term without parturition, and continued this typical gestation behavior for about two weeks after the normal date for parturition. It is reported by the attendants that this female has shown pseudo-pregnancy several times.

About 90 days after breeding females begin to undergo certain alterations, both physically and behaviorally. The physical alterations are especially difficult to observe. The only really obvious physical alterations are the changes in the abdominal area. Upon close inspection it can be seen that the nipples protrude more than normally. The females's general activity level is higher, after about the 90th day of the gestation period. Also, females sometimes become somewhat bellicose with other females at about this time.

TABLE 5

Lengths of gestation periods of five females picked at random

Each female had had at least three parturitions

	NUMBER OF FEMALE				
	1	2	3	4	5
1st gestation period......	100	106	108	111	108
2nd gestation period.....	112	111	108	110	110
3rd gestation period......	111	109	114	110	113
4th gestation period.....	112		110		
Range of days...........	12	5	6	1	5

At 100 days (occasionally varying four or five days either way) the gestating female is brought into one of the barns and isolated in one cage. In a few days certain behavior patterns appear which are peculiar to the late gestation period.

Generalizations from observations of gestating females are difficult to make. The patterns which are displayed by these females are highly variable. Several performances seem to be somewhat more persistent than others, and seem to be common to all females during the pre-parturition period. For example, pulling hair from the belly, rubbing the hind quarters against the belly, and pushing on it with the nose, all seem to be characteristic. Patterns of general restlessness are variable from animal to animal. Some females show all the signs of "upset" whenever a human is close. Some females, on the other hand, were completely complacent. At no time, however, are they incapable of vigorous action.

Fox (11), Tinklepaugh and Hartman (30), and others have studied parturition in certain primates. In general, such investigations have revealed the parturition process to be relatively long, and complicated by certain dexteral processes. In the lower orders less work has been done on this subject. For example, no adequate descriptions of parturition processes in the domestic cat are available.

Actual parturition has not been observed in the present study. The great variation (fourteen days) in the length of gestation periods makes it exceedingly difficult to observe particular parturitions. Furthermore, with few exceptions, all of the El Monte farm parturitions have taken place either late at night or very early in the morning.

On one occasion, observations were made of the gestation activities of a female immediately previous to parturition. The observations were the "closest" to actually observing parturition in the entire investigation. They began at 7:00 p.m., and lasted until 3:30 a.m. The cubs were evidently born, according to the attendants, at about 5:00 a.m. These observations will be transcribed here as they were actually made. In as much as the actual delivery took place so soon after the observations were stopped, of course, part of the actual parturition patterns are included in these notes. It is highly probable that actual delivery is not essentially different from certain of the observed processes described in the notes which follow.

October 17, 1939 (7:00 p.m.). "She was quiet for about one hour, except for very heavy breathing and heaving (abdominal). Began to change her position frequently. Then she turned on side and began vigorously pulling out hair around nipples with incisors. Then she gave a "spitting," gagging response, grimaced, and showed a little foam at mouth. Got up and began pacing; then roared, and started whole farm roaring. Paced and gave short "roar-like" grunts approximately every other time she turned around. Does not seem to especially "favor" hind quarters. Started roaring while pacing—stopped pacing and began to roar louder; then stopped, and her abdominal wall muscles contracted vigorously. Lay down on side at 8:22; then turned over on back with paws dangling, and remained very quiet. About every five minutes she gives a low growl. Whenever she turns over on back she extends hind quarters. At 9:00 she went into a squat-position, with legs (both front and rear) wide apart. Got up after about twenty seconds and began pacing, and growling. Squatted again, bent head forward, placed back against the wall, and licked genitalia profusely. Began pulling hair from nipples again—was more successful this time (more hair came out this time than before.) Her vaginal orifice was secreting fluid (appears to be blood) rather profusely. At 9:15 began to "knead" abdomen by pushing nose into it and then pulled more hair. The vaginal orifice is much distended now; much more than twenty minutes ago. Paced and groaned frequently till 9:45. At 9:50 squatted again, but for a longer period this time; more abdominal contraction. Began pacing again. At 10:10 licked genitalia and pulled hair. Abdominal contractions were much more intense and the labial wall, anterior to orifice, rose and fell considerably. At 10:40, stopped pacing and licked genitalia; began pacing again. Stopped pacing at 11:05, licked genitalia and pulled hair, squatted, during heavy muscular contractions. She turned around, smelled spot upon which she had been squatting and then raked up straw over spot. Paced again until 11:45. During the last two times she squatted, besides there were several convulsive body jerks, and a doubling up, in which her tail shook up and down rapidly at the root. At 11:50 she lay down, rolled over on back, then over on side, then closed eyes. At 11:55 rose quickly, licked genitalia, pulled hair. Then squatted, and a few drops of liquid (white, this time) were secreted. Then paced again. At 12:17 squatted again—"suction sound" heard; again a few drops of white fluid secreted. She immediately turned and licked the secreted fluid. Does much chewing and gagging; almost regurgitated. After licking genitalia she often shows the "sneeze-like" grimace, characteristic of males during sexual excitement. Is either licking genitalia or pulling abdominal hair continually; also pulls hair on end of tail frequently. At 12:55 she got up and licked genitalia, pulled hair on abdomen, moaned, paced. Hind quarters are wet from sitting down on spots where she has secreted. Squatted again for brief period, then paced, then again squatted. She almost always squats facing the light. Squatted again at 1:50; tail is curved up at root now. From 1:50 to 3:30, no squatting. After 1:50 she paced a little, then lay down. Has been breathing heavily. Occasionally, between 1:50 and 3:30, she has paced briefly, and "moaned" occasionally. There is some foetal movement. She has been lying laterally on floor, with head flat, for some time. (3:30)

October 18, 1939. "Apparently had parturition about 5:00 a.m. Attendant said that cubs were dry, and after-birth gone, at 7:00 a.m. She is lying with back to light, so that cubs cannot be seen. She would not come out of parturition cage to eat today. Seems to be sleeping most of the time. Cubs are nursing. There are two cubs."

In this parturition, as in others, the time between delivery of the different cubs in the litter was apparently very short. Borggreve (3) cites a case in which a lioness gave birth to three cubs. Five days after the birth of the first two, the third was delivered. One of the first two born died in three days, but the other two survived. But long intervals between deliveries seem to be extremely rare.

It is apparent that the parturition process is quite variable. Inasmuch as the actual act of parturition has not been observed, further comments cannot be made.

The length of the gestation period has a relation to the responses that infants are capable of performing immediately after birth. This is particularly noticeable in the case of eye-opening. If cubs are born on the 110th day their eyes are ordinarilly open on the fourth day after birth. In cases in which the gestation is less, (e.g., 106 days) the eyes usually open proportionately later. Likewise, the cub's eyes may be open at birth if the gestation period is unusually long. Though there has been no way of measuring general activity level, it appears that cubs from a long gestation period are more active on the first day after birth, than first day cubs from a short gestation period. Whether or not the eyes are open has a decided relation to general activity and body movements.

Several descriptions will be given here of reciprocal mother-cub response situations. In general, new-born cubs are extremely inactive, the most persistent activity being that of nursing. Moreover, conditions for careful observation are decidedly difficult during the first few days following parturition, since the mother usually keeps the cubs far back in the cage, or they are obscured completely by her body. These descriptions are made in terms of time from parturition; not gestation period length.

Description of One-Day Cub and Mother. "This litter consists of two cubs; one still-born, the other apparently normal. (Mr. Gay thinks the mother is in bad physical condition, and accounts for this by her exceptionally long gestation period.) The mother does not overtly respond to either the live cub or the dead one (which has not been removed from the cage yet). The live cub, lying on its abdomen facing the mother, is persistent in nursing. The mother's eyes are open from time to time, and when they are open her head weaves from side to side, as though she lacked balance. She has not overtly responded to general farm roaring.

A mother with two older cubs was just put into the next cage. The female under observation did not get up, but she lowered and extended her head, her eyes were dilated, and she raised her ears into an erect position. The infant still is nursing; definite oral responses are observable. The infant's head occasionally moves laterally while nursing, and its ears also become erect frequently. It keeps its hind legs doubled and its paws against its mother's abdomen. Occasionally, its fore-paws are drawn under its body. The infant's nose is pushed far into the hair on the mother's abdomen, and its lower jaw moves up and down rather rapidly; these mandibular movements are not vigorous. The infant rights itself with its front legs, but it can not get leverage with its hind legs. It is able to raise itself hesitantly on its front legs. The mother licked the infant vigorously on its back and on the back of its head. This knocked it away from her nipple. The cub responded by pulling strokes with its front legs, and uncoordinated pushing movements with hing legs in returning to mother's nipples. This was exceedingly vigorous. The cub struck at its mother's nose while she licked it. Its back sagged while it pushed up to the mother, its body being lifted from the floor by its front leg action. The mother is very slow and "careful" in all her movements in the cage. She is especially "cautious" in movements of her back legs. The infant shifted from back to front nipple, negotiating this by strong, pulling strokes. The mother dropped her hind leg on the infant's head while it was nursing a back nipple; the infant twisted its head and got free, while still holding on to the nipple.

At feeding time the mother did not get up and did not respond to the attendant with food for her. When the cub is asleep it twists a great deal, predominately in the hind quarters. While the mother licked the cub, it snarled considerably. This consisted in wrinkling its face, curling its tongue, opening its jaws, straightening out its neck and head (with the body), and curling back the lips, especially the upper lip."

Description of a Mother and Two-Day Cubs. "There are four cubs in this litter. This morning they are all lying tangled together in a corner. Each has his head bowed ventrally; and its hind legs pulled up under its body. They breathe spasmodically and heavily. Their hind quarters twitch a great deal during sleep. They usually lie on their abdomens, but also on their sides.

The mother got up, went to them and began to lick them. As each infant awoke it snarled. One climbed on top of the other three and went to sleep. (So far as can be seen from this position the eyes of all four cubs are still closed.) This cub used its front legs almost exclusively in climbing on others. Upon awakening there is a tendency to pull the head far down ventrally and to extend the forelegs; the claws can then be seen. While asleep one cub shows much lip and sucking movements. One cub lifted its head and "tried" to open eyes; did so slightly; a gray slit was visible. In doing this it extended its head upward at the peak of which this opening was observable.

They all show considerable tail movement The mother's licking is focused on the anal regions, primarily. Another cub has its eyes open now. Crawling movements with the fore-legs and pushing movements with the rear legs are quite evident. The mother awoke them again by bending over and licking them. One by one, they stretched, snarled, yawned and began to move about. Then the mother lay down close by and they crawled to her nipples and began to nurse. She then licked each in turn. One cub, with eyes almost closed, is attempting to nurse another; there is much random nuzzling. As they nurse, they knead considerably, but less than domestic kittens. The infant's nursing brings noises something like grunting and high "gurgling." They fight each other considerably while they are nursing, mostly by pushing with their noses, but also by striking and pushing with their front paws. This is well coordinated activity. In this, and other cases observed, the mother's hind leg slowly drops on the infants when her eyes close. When there is an outside noise, her eyes open and her leg rises gradually. After about thirty minutes of nursing, she got up and the cubs crawled into a knot and went to sleep. When she got up, one cub held on to a nipple, even until she started walking; its tail almost touched the floor: (this is the most belligerent cub in the litter). She kicked it loose with one of her hind feet. Before the cubs went to sleep, they licked their lips. After the nursing period it was about twenty minutes before they were completely asleep again."

Description of Three-Day Cub and Mother. "(The same cub and mother, as described on *first day* above, were observed on the third day after parturition.) The cub's eyes opened yesterday (second day). Its head movements today are more coordinated (body-eye coordination?). It snarls when its mother's leg comes abruptly toward it. The mother turned the cub with its hind quarters toward her and licked its back, then around its anal regions. The cub has some control of its tail; i.e., it can move it at the root but have seen no indication of muscle action in the middle part of the tail. In order to move at all by using its hind quarters, it has to move both hind legs together. The fore-quarters are decidedly more active, strong and coordinated than are the hind. The mother continues to lick its anal region. The infant's cord is still hanging to its abdomen. There is much random nuzzling by the infant. It worked its way back from her head, where she had been holding it while she licked it, to her nipples; all the way there was much random nuzzling. The cub's orientation to nipples seems quite precise.

The mother has become quiet restless; paces some. She roared during the general farm roaring. The infant was lying in front of her while she was roaring; it wiggled its head considerably. It continued to do this while she roared, then finally lifted its head and turned it away laterally."

Descriptions of Fourth-Day Cubs and Mother. "Throughout the day sleeping is the most frequent activity. The two cubs of this litter remain far back in the darker corner. They sleep on their sides mostly, but lie on their abdomens more than the one and two day cubs. Their rear legs twitch much during sleep. Also, they both show definite sucking movements during sleep; also lips curl up and then relax frequently. They can right the front part of their bodies with their forelegs, but have great difficulty in doing anything with their hind quarters. Their lateral head movements are frequent, but they do not lift their heads back very much. The most frequent specific response is the snarl. It is set off by most any stimulation: noise, change in light, movement by the mother, even their own movements. They nuzzle each other considerably and go through typical nursing activities when in contact with each other's bodies. When one's nose is against the other's body, and nursing responses begin, it frequently "kneads" the air. During this activity, its claws may be seen to retract and extend. There is also flexion of the carpal bones. (This indicates the early functional development of claw action.) The mother growls a great deal during nursing. She holds her hind leg up for long periods. When her cubs are crawling over her paws and nuzzling, she emits low growls, and bares her teeth, but does not bite at them. It appears that these cubs are more generally acitve than younger ones observed. Their eyes are wide open." In some cases mothers refuse to care for their cubs. In such instances the cubs are removed from them and raised by hand. However, this refusal is infrequent, usually occurring when there is only one cub in the litter.

From sixty-four parturitions, 159 cubs were born. This results in an average of 2.48 cubs per litter. There are from one to four cubs in a normal litter. Litters of five cubs have been known. Two such occurred at El Monte during approximately two hundred parturitions. Occasionally, mothers eat their young. In the three years since the present investigation has been going on, this has happened only once. Apparently, it happens when the mother is eating the after-birth. She evidently keeps on eating, devouring the cubs in the process. In the case that happened during the present study, the attendant reported that all the signs of a parturition were present when he came to the cage in the morning, but no sign of any cubs. Refusing to care for cubs, or eating the litter, happens with first-time mothers more often than with mothers that have delivered litters before.

The infants that are raised by hand show certain differences from the mother-raised cubs. In general, of course, they are considerably tamer. While the mother-raised cubs stay far back in the cage when a human comes close, the hand-raised cubs do just the opposite. Most noticeable of all these alterations, is the dropping out of the snarl when cubs are brought to the house to be raised. The snarl becomes very infrequent. Also, the nursing responses which are called out by the nuzzling-contact with other's bodies in the mother-cub situation, are soon lost in the hand-raised environment. Pacing, in terms of definite feeding times, is begun sooner in the hand-raised situation than in the mother-raised situation. In the latter case there is no particular feeding schedule. When two or more cubs are hand-raised together, their play responses are quiet similar to those of mother-raised cubs. When cubs are hand-raised individually, they develop certain play patterns which are directed usually toward objects in their pen. This consists, mainly, in chewing, rolling over, biting, clawing, and tugging.

The cubs are usually taken from their mothers, under normal conditions, at from four to six months. By this time they have been started on a regular meat diet. Within a few weeks after this new diet is begun, minor fights between cubs occur daily. Occasionally the cubs persist in attempting to take away the mother's meat from her. This often gets to the place that the mother cannot eat her food, without finally cuffing one or more of the cubs severely. Soon after this new regime, it is necessary to separate the mother from the cubs during feeding time, and feed the cubs by themselves.

The activities which take place during gestation, parturition, and the early mother-infant development period are of great importance, and deserve careful investigation. The foregoing does not aim to be more than a survey of some of the more obvious behavior during this period. It may serve, however, as a basis for further investigation of these same functions, not only in *Felis leo*, but also in other species of the genus *Felis*.

VII. Characteristics of the Lion Cub

This section will deal briefly with two aspects of cub behavior. First, particular functions which are certain to make their appearances in all felines will be enumerated, briefly described, and roughly placed as to time of appearance. Second, a general description of a particular "social" situation will be given.

The concept of maturation has been variously described and employed. It may be assumed from experimental evidence ". . . that there is a hierarchy of internal regulatory factors that control cellular growth and functional organization from the moment the ovum is fertilized until adult life is reached. To development that is *primarily* so regulated, the name *maturation* is given nowadays in order to set if off from other processes by which response mechanisms are acquired, particularly those designated by the term learning" (26). Some of these responses, which may be regarded as due primarily to maturation, have been observed and can be summarized as follows:

(*a*) *Crawling-approach.* Includes any responses which direct the entire body anteriorly. The first responses of this nature are negotiated largely by the front legs; e.g., crawling to nipples of mother. This response is present on the first day.

(*b*) *Crawling-retreat.* Includes responses which direct the head away from a former position or some object. It is possible for the cub to turn away, pivot (the rear quarters down) on the first or second day. Actual crawling backwards is not negotiated until the sixth or seventh day. The hing legs cannot lift the hind quarters from the floor until then (this being required for the response).

(*c*) *Lateral movements.* This includes any lateral (complete) body movements. This sort of turning away (lateral) employing sidewise pushing by *one* of the legs, appears on the first or second day.

(*d*) *Mouth-sucking movements.* This includes responses of the lips and tongue when the muzzle is in contact with a furry object or a nipple; sometimes it may be seen in sleep. This response is functional immediately after birth.

(*e*) *Synergizing reactions.* These include coordinated movements of the head and body; that is, responses which are made in terms of some stimulus field and which are fairly well coordinated. Head and bodily movements of this sort are not present until the fifth to eighth day.

(*f*) *Coordinated escape movements.* These coordinated responses include only responses which employ the body as a whole, in escape. Such responses are not present until about eleven to fourteen days of age; the necessity for adequate functioning of the rear quarters delays this.

(*g*) *Eye-opening.* This includes contraction of the eye-lid muscles so that the conjunctiva may be seen by the observer. This has been observed as early as a few hours after birth, and as late as six days.

(*h*) *Head and body movements* (in relation to eye-opening). Includes any responses that are coordinated with vision. The first such responses seem to be general body orientation away from the light. These were first observed at from one to six days.

(*i*) *Snarling.* This response includes rolling the tongue back, (extension and ducking of the head comes later,) opening the mouth, and drawing back the lips. This response has been observed as early as the first day. Many stimulus patterns may set it off, e.g., touch on the head.

(*j*) *Hissing.* This response includes the responses under (i) plus an audible exhaling of air. It is probable that cubs really hiss when they *first* snarl, but the exhaling of air is not audible at this time. It can be heard at about nine days.

(*k*) *Defensive and offensive striking.* These responses can not really be broken up into single acts. Offensive and defensive striking have been observed in two-day cubs while they were nursing.

(*l*) *Sitting.* This consists in holding fore-part of body up with the front legs while the hind-legs are collapsed. Such has been observed as early as five days. A cub of two days can keep its head and anterior part of its trunk off the floor, though this is not actually sitting up.

(*m*) *Righting.* This includes any responses which accomplish the function of turning on the "accustomed" side of the body, the ventral side. Often when the mother licks the cubs, she rolls them over on their backs, and they can right themselves on about the second day. This is accomplished as soon as the appendages are motile enough to push against the floor strongly enough to roll the body over.

(*n*) *Walking*. Coordinated, erect movements of all four legs by which the body is moved, and the trunk and head kept off the floor. This cannot be negotiated until about from the tenth to fifteenth day. The back sways considerably for some time, even after this is accomplished.

(*o*) *Scratching*. A rapidly negotiated, "circular" response by one of the appendages in contact with some part of the body. The animals are kept quite free from insects (other than flies, which seldom bother cubs) and may have no occasion to scratch. The observer has not been able to elicit this response by artificial stimulation.

(*p*) *Running*. Arbitrarily described for the present purpose as "fast walking." It is never present until about twenty-fifth to thirtieth day. Even then, it is usually cut short by a hind quarter collapse.

(*q*) *Biting*. Includes responses of closing jaws on some object, or part of an object (distinct from sucking). This does not seem to appear until the teeth begin to push through the gums, at about twenty-one to thirty days.

(*r*) *Clawing*. Includes any indication of retraction and extension of the claws. While nursing, cubs knead the mother's breasts. This starts on the first day. It is always accompanied by functioning of the claws.

(*s*) *Washing*. Consists in licking any part of the body. This has not been observed in cubs less than about thirty days of age. Cubs of two days have been observed "licking" their lips after nursing.

(*t*) *Head turning in response to auditory stimuli*. Includes coordinated head turning in response to noises. Observation of head movement (and snarling) in response to loud hand clapping close to the cage has been made of second-day cubs. It has not been observed as a coordinated response in terms of the stimulus source, however, until the eyes are open, from about one (or two) to six days.

(*u*) *Use of claws in climbing*. Includes any responses which employ the claws to pull the body up to a higher level. Lions seldom climb, in the usual sense, though they do sometimes pull themselves up on things. This has been observed in cubs as young as about thirty days.

(*v*) *Vocalization*. There are several types of vocalization, in addition to the hissing noise. The earliest of these to develop is a low "meow," which is usually present at about thirty days. At about sixty days the explosive bark develops (but lasts only about twelve months). The "meow" drops out usually at about 10 to 12 months of age.

(*w*) *Tail movements*. Includes any movements of the tail which are made without moving another part of the body. Lateral "switching" of the tail has been observed as early as the second day. However, more complicated tail movements do not appear until later. For example, circular motions of the tail appear about the time actual play begins. Cubs frequently whip their tails around in a circle just prior to springing. This was first observed at about forty-five days. The final development of tail movement, which is the movement of the tip only, (in various ways,) and bending the tail part way down, may not appear until about twelve months.

In order slightly to amplify the information on these developments, brief descriptions of certain arbitrarily designated phases of behavior will be given here.

These will include: play behavior, activities related to food-getting, fighting, early sex behavior, early indications of docility, and responses of "thyroid cubs."

Cubs show much more general activity than do mature animals. They do not play as persistently as might be thought, however. For example, they probably play about one-fourth as much as do domestic kittens. Play behavior of cubs may be characterized as a series of performances consisting of rolling, biting, clawing, and hanging on with their front feet while kicking with their back feet. Flight and pursuit are much less frequent with lion cubs than with domestic kittens. Inasmuch as there is a marked developmental retardation of the hind quarters, running is frequently cut short by the fact that the cub's hind quarters collapse. As they grow older, stalking and rushing at each other from behind objects becomes comparatively frequent. Climbing upon objects is rather common, and when two or more cubs are together, they often play "king of the mountain," during which one cub climbs upon some object and the other cubs attempt to dislodge him.

As a generalization, play seems to be a system of responses in which each cub directs its responses to another particular cub, and persists in responding to this particular cub over a considerable length of time. The cub to which this one's responses are directed frequently pays no attention to these responses at all, and, in fact, may be responding to still a different cub. While domestic kittens are known to shift their play attacks from one kitten to another very rapidly, when a lion cub plays, it plays with one other cub, to the exclusion (in terms of attention) of all the others.

Responses of hand-raised and mother-raised cubs in relation to food-getting already has been discussed. Following this early period, cubs are taken from their mothers and from the house (at about five months) and put together to form a year group. Soon after this new environment is created for the cubs, relatively specific patterns of responses build up in relation to food-taking. At first, it is difficult to get the cubs to come into the feeding cages from the lot. However, within about ten days, they come in as soon as the attendant opens the gate. And within the next two weeks, they show typical pre-feeding pacing, just prior to feeding time. (They mill back and forth in front of the gate.) During this pacing, cubs of this age usually vocalize some. They sometimes "meow" in an individual rhythm consistent with this pacing. At the same time, they are learning to go to particular compartments and wait to be locked in them before being fed. Cubs of this age remain far back in their individual compartments and respond for the food much as do the older animals. During this process, their vocalization is altered to a series of explosive "barks," and it is clearly evident that the entire food-taking process is of high emotional quality. These patterns, once set up, begin to merge into the typical processes of the adult animals, described earlier in this paper.

Fighting can be mentioned here only for its conspicuous absence. Occasionally one cub may strike at another, but it has not been observed that the other responds in kind. Actual fighting has not been observed among lion cubs.

Soon after a year group is formed, some cubs begin to show dominance over the others. These dominant cubs are usually the largest ones in their groups, and most frequently are males. Dominance is displayed in various ways. Dominant cubs almost always are the first to push through the gate when it is opened to admit the group to the feeding cages. Also, quite often, dominant cubs suck and chew on the tails of other cubs. Another type of dominance response is that of feigned coitus, in which a dominant young male singles out another cub and mounts it. It is not known whether this behavior is always directed toward females; it appears that it is not. Feigned coitus is usually not demonstrated until about six or seven months, but in one case it was observed in a cub of only two months.

Certain cubs begin to show abnormality in structural development at about eight weeks of age. This somewhat frequent condition has been diagnosed as "hypo-thyroidism." It is apparently the only growth abnormality which has been detected in cubs. In general, it consists of a "stubbiness" of all the body parts. The muzzle is short, the eyes are bulging, the body is short and heavy, the appendages are short and thick, and the hair is coarser in quality than that of normal cubs. Flies frequently light around the eyes of these cubs. Such cubs seldom engage in play, and are very much less active than normal cubs. These abnormal cubs are never amenable to human handling. Attempts by the trainers to touch them (which is almost always possible with normal cubs) are met by volleys of explosive barks, and by hisses, snarls, and vigorous attempt to escape. So complete is their intractability that, soon after the abnormality appears, the cubs are disposed of. On the basis of the present observations, no significant comments can be made upon these cases. But it may be said that they warrant further study. Evidently there is a very real relation here between certain physiological conditions and certain levels of behavior.

At this point a brief description will be given of a situation in which three cubs (litter mates) were introduced to a group of cubs that had been together for several weeks. This original group consisted of seventeen cubs, about five to seventeen months of age, and approximately equally divided as to sex.

The larger members of this group tended to be dominant in "social" behavior. The morning of the day the observation was made, one young male in particular persisted in sucking and chewing the tail of a smaller animal. The latter growled and struck at the larger frequently. When this remonstrance became very vigorous, the aggressor would either tug on the tail and pull the smaller animal back into position or would cuff it into submission. Once when the tail chewing became very rough, the victim cub apparently turned to nip his aggressor. But the feet of a third, non-participating animal were nearby and were attacked instead.

To this group were introduced three siblings, about five months of age, who had been with their mother since birth. On the day that they were taken from their mother, they were put into one of the compartments of a series which housed the seventeen just described. However, they were not put into actual contact with the group that day. On being housed in a new environment they demonstrated great excitement. On the next day very similar patterns of excitement were observed. On the third day, after feeding time, a gate was opene that allowed the three to join or be joined by the members of the original group

At first, the three made no attempts to leave, and remained as far back i their compartments as possible. The other animals showed almost immediat "interest" in the new cubs. The larger ones left the lot, where they had been put after being fed, and returned to the series of cages (the doors of which wer now open, making one large cage). The incoming cubs began "investigating. One of the three new cubs sneaked into the adjoining compartment and la down in a rear corner. Just following this, one of the dominant males of th original group walked into the compartment where two of the new comers were However, he was met with such a volley of barks, spits, and vigorous defens gestures that he "shot" back through the same door by which he had entered and returned to the lot. Next, another male (judged by the observer to be slightly less dominant than the first, just mentioned) came in from the othe direction, and was met by a similar defense response from the new cubs. It too retreated and returned to the lot.

Meanwhile, several of the original group had climbed up the run-way to the compartment in which two of the new cubs were standing. They also were met by hisses, growls, etc. However, the investigators remained nearly motionless until the growling had practically stopped. These two cubs then proceeded into the compartment. When the growling which this occasioned had subsided, another of the original group came in, but no remonstrances were made this time by the cubs.

After much rubbing, "smelling," etc., one of the original group went to the door and stood for some time. By now, all the original group had either come inside the compartment or had climbed on the run-way leading to it. One of the new cubs now looked out into the lot for the first time. Finally, it slowly began to follow one of the original group out onto the run-way. When it started to walk down the abruptly descending run-way, its feet began to slip. However, it was able to pull itself back up into the compartment. A second, more successful, attempt was made. By the third attempt, it managed to get down into the lot. By this time another of the new cubs was also attempting the same thing and was soon outside.

The first new cub to descend into the lot, was "greeted," and "smelled," and rubbed by most of the original group. It was a female, and was immediately pursued by one of the large, dominant male cubs and subjected to feigned coitus. This was only momentary because of its defensive responses. Following this, it paced up and down the fence line several times, followed by most of the group. When it was able to get back to the run-way, it scurried back up into the compartment. This was followed by what might be called "practice" attempts at descending and ascending. The third new cub remained in its compartment for some time. It was "greeted" on both sides by members of the original group. Finally, it stopped remonstrating, got up, went to the run-way, and descended into the lot. A very long time was required for this cub to lose its belligerant behavior. It is interesting to note that this cub is a very bad "thyroid case."

It may be seen from the foregoing account that there are certain factors which complicate the individual-to-individual responses of lions. As was pointed out in the section on "Adult Fighting," unfamiliar objects seem to call out both offensive and defensive responses. The significance of these factors can be realized better when it is understood that even in cubs this sort of behavior is in evidence.

SUMMARY

This study has included an investigation of two primary information sources: (1) material in the literature, and (2) data obtained by direct observation of captive lions, at the Gay Lion Farm at El Monte, California.

An examination of the available recorded accounts of lions revealed very little information on specific details of the behavior of lions. A few of these accounts, however, presented notions concerning lions which were useful in shaping this exploratory investigation. The major area of attention has been devoted here to descriptions of the observational findings from the Gay Lion Farm.

The direct observational part of the study involved preliminary observation of the captive conditions and routines imposed on the animals by the operators of the farm, and the response patterns of the animals in terms of these. Further systematic attempts were made to discover the types of behavior which could be studied most adequately and profitably by observational non-experimental techniques.

Following the preliminary period of study, the animal's activities were arbitrarily divided into seven categories of behavior: (1) Activities preliminary to and following feeding; (2) Training; (3) Vocalization; (4) Adult play and fighting; (5) Sex activities; (6) Gestation, parturition and infant care; and (7) Characteristics of the lion cub. These behavior divisions were then studied observationally.

It is apparent from a study of this nature that proofs and conclusions are not forthcoming. Only a relatively long-range objective can justify such a study. The imponderables of any division of investigation can eventually be solved only when the isolated and divergent fragments have been made available.

This study has tended to indicate throughout that most response systems, usually deemed fundamental, are, even under these rigid conditions, highly variable. It has been seen that such response systems as have been described, may be negotiated in a number of ways. The material presented also suggests that such vague terms as those of "wildness" and "ferocity" frequently used to describe infra-human behavior capacities, probably are interpretive constructs, having little relation to the organism concerned. Finally, it has indicated that some of the response systems observed might profitably be studied under carefully controlled experimental conditions.

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